THE NAUTILUS

QL
401
.N314
IZ

Volume 135, Number 1
May 13, 2021
ISSN 0028-1344

A quarterly devoted to malacology.

SMITHSONIAN
SEP 27 2022
LIBRARIES

EDITOR-IN-CHIEF

José H. Leal
The Bailey-Matthews National Shell Museum
3075 Sanibel-Captiva Road
Sanibel, FL 33957 USA

EDITOR EMERITUS

M. G. Harasewych
Department of Invertebrate Zoology
National Museum of Natural History
Smithsonian Institution
Washington, DC 20560 USA

CONSULTING EDITORS

Rüdiger Bieler
Department of Invertebrates
Field Museum of Natural History
Chicago, IL 60605 USA

Arthur E. Bogan
North Carolina State Museum of Natural Sciences
Raleigh, NC 27626 USA

Philippe Bouchet
Laboratoire de Biologie des Invertébrés Marins et Malacologie
Muséum National d'Histoire Naturelle
55, rue Buffon
Paris, 75005 FRANCE

Robert H. Cowie
Center for Conservation Research and Training
University of Hawaii
3050 Maile Way, Gilmore 409
Honolulu, HI 96822 USA

Kenneth A. Hayes
Berniece Pauahi Bishop Museum
Honolulu, HI 96817

Steffen Kiel
Department of Paleobiology
Swedish Museum of Natural History
Box 50007
104 05 Stockholm, SWEDEN

Harry G. Lee
4132 Ortega Forest Drive
Jacksonville, FL 32210 USA

Charles Lydeard
Biodiversity and Systematics
Department of Biological Sciences
University of Alabama
Tuscaloosa, AL 35487 USA

Bruce A. Marshall
Museum of New Zealand Te Papa Tongarewa
P.O. Box 467
Wellington, NEW ZEALAND

Paula M. Mikkelsen
Paleontological Research Institution
1259 Trumansburg Road
Ithaca, NY 14850 USA

Diarmaid Ó Foighil
Museum of Zoology and Department of Biology
University of Michigan
Ann Arbor, MI 48109-1079 USA

Gustav Paulay
Florida Museum of Natural History
University of Florida
Gainesville, FL 32611-2035 USA

Gary Rosenberg
Department of Mollusks
The Academy of Natural Sciences
1900 Benjamin Franklin Parkway
Philadelphia, PA 19103 USA

Elizabeth Shea
Mollusk Department
Delaware Museum of Natural History
Wilmington, DE 19807 USA

Ángel Valdés
Department of Malacology
Natural History Museum of Los Angeles County
900 Exposition Boulevard
Los Angeles, CA 90007 USA

Geerat J. Vermeij
Department of Geology
University of California at Davis
Davis, CA 95616 USA

SUBSCRIPTION INFORMATION

The subscription rate for volume 135 (2021) is US $65.00 for individuals, US $102.00 for institutions. Postage outside the United States is an additional US $10.00 for regular mail and US $28.00 for air delivery. All orders should be accompanied by payment and sent to: THE NAUTILUS, P.O. Box 1580, Sanibel, FL 33957, USA, (239) 395-2233.

Change of address: Please inform the publisher of your new address at least 6 weeks in advance. All communications should include both old and new addresses (with zip codes) and state the effective date.

THE NAUTILUS (ISSN 0028-1344) is published quarterly by The Bailey-Matthews National Shell Museum, 3075 Sanibel-Captiva Road, Sanibel, FL 33957.

Periodicals postage paid at Sanibel, FL, and additional mailing offices.

POSTMASTER: Send address changes to: THE NAUTILUS
P.O. Box 1580
Sanibel, FL 33957

THE NAUTILUS

Volume 135, Number 1
May 13, 2021
ISSN 0028-1344

CONTENTS

Walter E. Meshaka, Jr.
Kenneth G. Rice
Oron L. Bass, Jr.
J. Hardin Waddle
Demographic responses to density-dependence by two populations of the Florida Tree Snail, *Liguus fasciatus* (Gastropoda: Orthalicidae), in Everglades National Park 1

Alan R. Kabat
Richard Irwin Johnson (1925–2020), a life well lived 11

RESEARCH NOTE

Licia Sales
Vinicius Queiroz
Rudá A. Lucena
Alvaro E. Migoto
An unprecedented observation of the nudibranch *Spurilla braziliana* (Gastropoda: Aeolidiidae) as a food resource of the pycnogonid *Pigrogromitus timsanus* (Arthropoda: Ascorhynchoidea) 32

Demographic responses to density-dependence by two populations of the Florida Tree Snail, *Liguus fasciatus* (Gastropoda: Orthalicidae), in Everglades National Park

Walter E. Meshaka, Jr.
Section of Zoology and Botany,
State Museum of Pennsylvania
300 North Street, Harrisburg,
PA 17120 USA

Kenneth G. Rice
U.S. Geological Survey,
Wetland and Aquatic
Research Center
7920 NW 71 St,
Gainesville, FL 32653 USA

Oron L. Bass, Jr.
26450 NW 166 Ave.
High Springs, FL 32643 USA

J. Hardin Waddle
U.S. Geological Survey,
Wetland and Aquatic
Research Center
7920 NW 71 St,
Gainesville, FL 32653 USA

ABSTRACT

During May–October 1996, we captured and individually marked and released Florida Tree Snails, *Liguus fasciatus*, from two sites, a subclimax hammock and a large isolated wild tamarind tree, in the Long Pine Key region of Everglades National Park. Populations shared the same two dominant morphs, *castaneozonatus* and *cingulatus*, both of which are strong colonizers. Monthly survivorship between the two sites were comparable, although annual survivorship was lower on the isolated tree. Intersite differences in growth rates were equivocal. The populations differed with respect to number of morphs, population size, and population structure. The hammock site was a subclimax hammock with a large and stable bell-shaped population structure comprising nine morphs. In contrast, the population structure of the single tree was highly skewed, with many young individuals produced, intermediate ages absent, and few large adults of larger asymptotic size present. Number of snails/m^2 was higher on the isolated tree. Demographic studies of the Florida Tree Snail are uncommon. Our findings corroborate certain aspects of the ecology of this species and clarify two different demographic responses, one of stability, and one of apparent resource limitation whose demography represents opportunities for colonization.

Additional Keywords: Ecology, age structure, population structure, growth, mark-recapture, host trees

INTRODUCTION

The Florida Tree Snail, *Liguus fasciatus,* is an arboreal tree snail found in tropical hardwood hammocks of Cuba, south Florida, and the Florida Keys (Simpson, 1929; Pilsbry, 1946). The ecology of Florida Tree Snails is poorly studied, with few recent studies using quantitative demographic approaches. Bennets et al. (2000a) studied host tree selection and movement probability (Bennets et al., 2000b) in a population in Big Cypress National Preserve. Brown (1978) and Jones et al. (1981) studied the population in the Long Pine Key area of Everglades National Park.

Although the species is extremely morphologically variable (fifty-eight morphs of *L. fasciatus* are recognized, of which some have become extinct), they are all in fact all members of a single species (Hillis et al., 1991). Some of the distinct morphs have been introduced into Everglades National Park (ENP) with the goal of protection from extinction (Jones et al., 1981). Florida Tree Snails are found exclusively in the hardwood hammocks of subtropical south Florida which themselves are found primarily in isolated remnants outside of the protection of ENP and Big Cypress National Preserve (Diamond and Heinen 2016). Tree snails are widely distributed in the tropical hardwood hammocks of ENP, where some morphs, such as *castaneozonatus*, occur in high frequencies (Jones et al., 1981).

In this study we examined population dynamics of the Florida Tree Snail in the Long Pine Key (LPK) area of ENP during one field season. We compared ecological responses of populations of the species from two structurally different sites on LPK to one another and to findings from other southern Florida studies on this species.

STUDY AREAS AND METHODS

Two sites were visited multiple mornings each month during April–October 1996 on Long Pine Key, Everglades National Park, Homestead, Florida. Two sites were sampled with very different situations. The first site, which we call Hammock Trail, was a trail through a tropical hardwood hammock located along a spur road that connected Royal Palm Hammock Road and Research Road (25.392640 / –80.621060). The same 100 m of the trail was sampled during each of the 18 visits (1–7 times per month in April, May, June, July and October). Tree heights associated with snail captures at Hammock Trail were measured in m from observations during April–October. Because mark and recapture did not begin before May, all other analyses used data collected during May–October.

Along Hammock Trail, trees associated with all snail captures were identified to species. This trail had been a road with a gate and was no longer maintained sometime before 2010 (Lori Oberhofer, pers. comm.).

The second site was a large wild tamarind tree, *Lysiloma latisiliquum*, located in front of the entrance station to the park, which was centered on a vegetated median strip between two divided road lanes (25.394551 / –80.590022). Its location in the middle of a highly traveled road and the presence of mowed swale between the road and nearby park habitat, we believe, made this an effectively isolated colony. We call this site Entrance *Lysiloma*. This site was sampled five times (once in May, June, July, September and October). Encounter heights of snails were not measured on this tree. Tree snails of both sites were removed from trees and individually marked with a number scratched onto their shell. The number was then traced with indelible ink and covered with clear nail polish. Shell length was measured in mm with hand calipers, and color morphs were identified when possible. Individuals were released in paper cups tacked 1.5 m above-ground to the tree from which they were captured. Recaptured snails were recorded, and all new snails were marked on each sampling occasion. All captures from both sites were pooled by month for analyses.

von Bertalanffy growth curves (von Bertalanffy, 1960) were fitted for both populations using SAS proc nlin (SAS Inst., 1988). In the model formulation, we used 18 mm as length at time 0, a size greater than that of a button snail (hatchling or recently hatched tree snail). We used the difference in shell length between successive re-captures to estimate the mean asymptotic length in the model (Fabens, 1965). Monthly distribution of body sizes provided another measure of growth rate by following growth trajectories of presumed cohorts. Age distributions were approximated by counts of resting lines on the shell, which are associated the end of a season's growth.

To estimate population abundance, snail capture probability, and monthly survival, we used the Jolly-Seber mark-recapture model as implemented in Program MARK ver. 9.0 (White and Burnham, 1999). This model assumes that all snails (both marked and unmarked) are equally likely to be captured each sampling occasion. It does not assume that populations are closed, so it allows for demographic processes such as births, deaths, immigration, and emigration to occur. We fit models that represented constant and sampling occasion-specific rates for survival and capture probability, and chose the best model using Akaike's Information Criterion. Model fit was assessed using Program RELEASE (Burnham et al. 1987). Monthly survival estimates were converted to annual survival estimates by raising them to the 12^{th} power. To estimate population density to facilitate comparisons between sites, we assumed that the width of the transect at the Hammock Trail was 0.5 m on each side and thus the area surveyed on the 100 m transect was 100 m^2. The diameter of the *L. latisliquum* comprising Entrance *Lysiloma* was approximately 1 m at chest height and 3.4 m in height. The tree was around 4.6 m in greatest width; therefore, we calculated the area of circle with radius 2.3 m to estimate the area surveyed at that site was 16.62 m^2.

RESULTS

Morph Distribution: Nine morphs could be detected along the Hammock Trail (n = 147), four of which were also found on the Entrance *Lysiloma* (Figure 1), where 61 were identified to morph. At both sites *castaneozonatus* was the dominant morph, followed by *cingulatus* (Figure 1).

Tree Species Use: Along the Hammock Trail, tree snails were recorded from seven tree species. Exclusive of 131 buttons, all of which were found on *L. latisiliquum*, the remaining 170 total captures were distributed among the following species: *Bursera simaruba* (0.59%), *Dipholes salicifolia* (42.9%), *L. latisiliquum* (41.2%), *Metopium toxiferum* (2.9%), *Myrica cerifera* (0.59%), *Tetrazygia bicolor* (2.4%), *Quercus virginiana* (9.4%). Snails occupied a wide range of heights on trees along the Hammock Trail (Figure 2). The modal tree height for tree snails was 250–299 cm, and 200–299 cm constituted 82.0% of all sightings (Figure 2).

Growth: We used capture data from 20 snails with multiple captures from the Hammock Trail population and 31 snails from the Entrance *Lysiloma* for our growth curve analysis. Shell length at last capture ranged from 23.4 to 43.1 mm shell length for the Hammock Trail and 21.6 to 61.8 mm for the Entrance *Lysiloma*. Buttons were detected along the Hammock Trail as early as each of the four May visits of 13, 14, 17, and 20 May associated with the beginning of the study. von Bertalanffy growth curves generated for both Hammock Trail and Entrance *Lysiloma* (Figure 3) assumed a "non-button" size of 18 mm shell length for size at time 0. Mean asymptotic shell length was 39.96 mm (95% CI = 38.57–41.34) in the Hammock Trail population and 56.18 mm shell length (95% CI = 32.05–80.30) for the Entrance *Lysiloma* population (Figure 3).

Growth rates were variable (Figure 4), but rapid as seen in monthly distribution of shell length in the Hammock Trail population (Figure 5). The presumed growth trajectories of the monthly distribution of shell length (Figure 5) indicated that snails of the Hammock Trail population hatched at 7.9–9.6 mm, were approximately 16–17 mm at one-year of age, 20–24 mm at two years of age, 33–35 mm at three years of age, 38–43 mm at four years of age, and possibly 46 mm at five years of age. Variation in growth resulted in some individuals reaching sexual maturity in time to breed in September before their fourth birthday the following May if 40 mm is the minimum shell length at sexual maturity (Brown, 1978). The scarcity of snails of older size-classes could be the result of mortality after the first breeding.

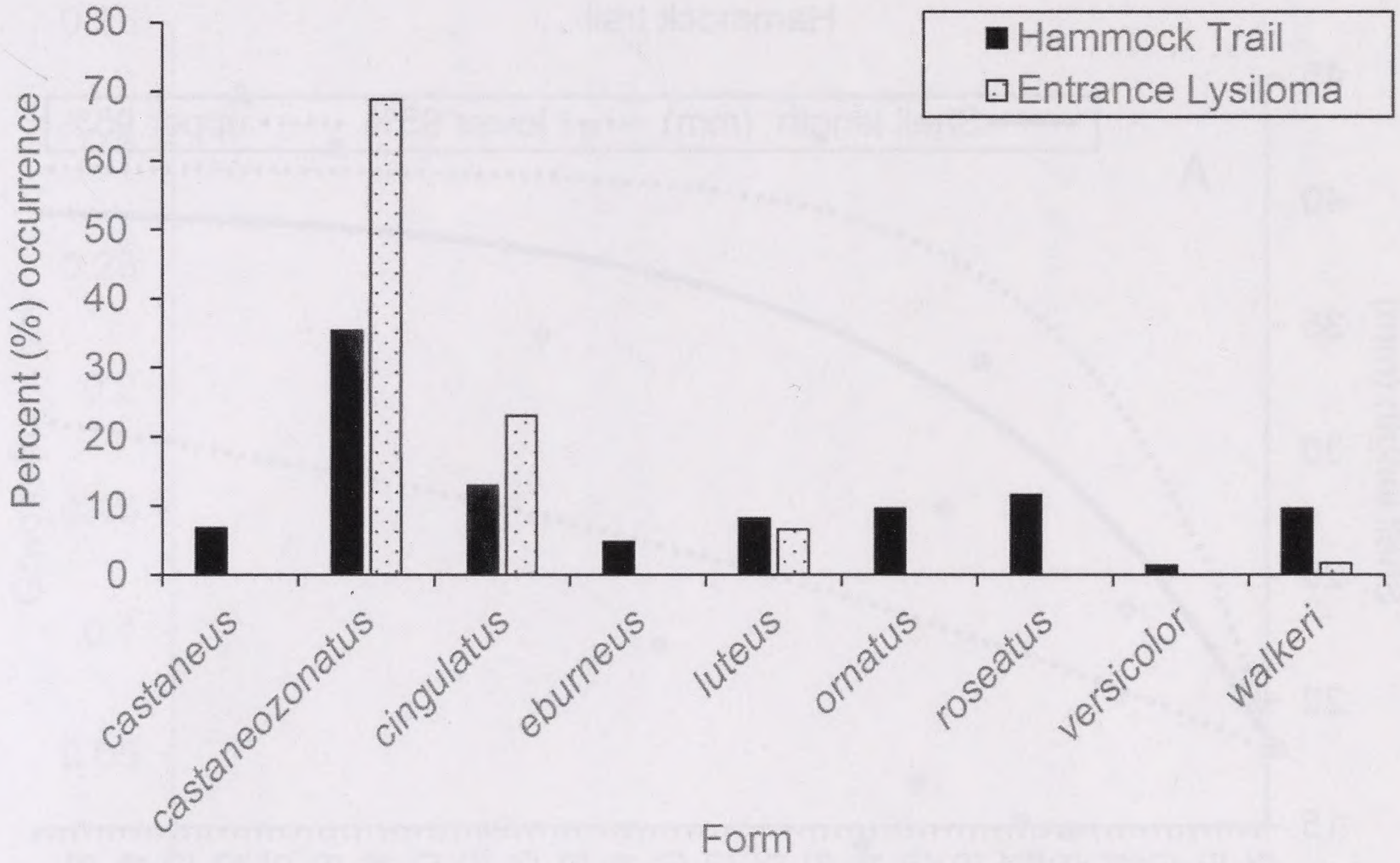


Figure 1. Percent occurrence of color morphs of the Florida Tree Snail (*Liguus fasciatus*) along Hammock Trail (n = 147) and on an isolated wild tamarind tree, Entrance *Lysiloma*, (n = 61) in Everglades National Park during May–October 1996.

The growth curve of the Hammock Trail population (Figure 3) predicted 27.0 mm at two years of age, 32.0 mm at three years of age, and 35.0 mm at four years of age, which were comparable to the shell size-age estimates derived from Figure 5. However, the model indicated an age beyond 111 months of age at the asymptotic length of 40.0 mm.

The presumed growth trajectories of the monthly distribution of shell length (Figure 5) indicated that snails of the Entrance *Lysiloma* population were approximately at least 20 mm at one-year of age and 30 mm at two years of age. The growth curve of the Entrance *Lysiloma* population (Figure 3) predicted

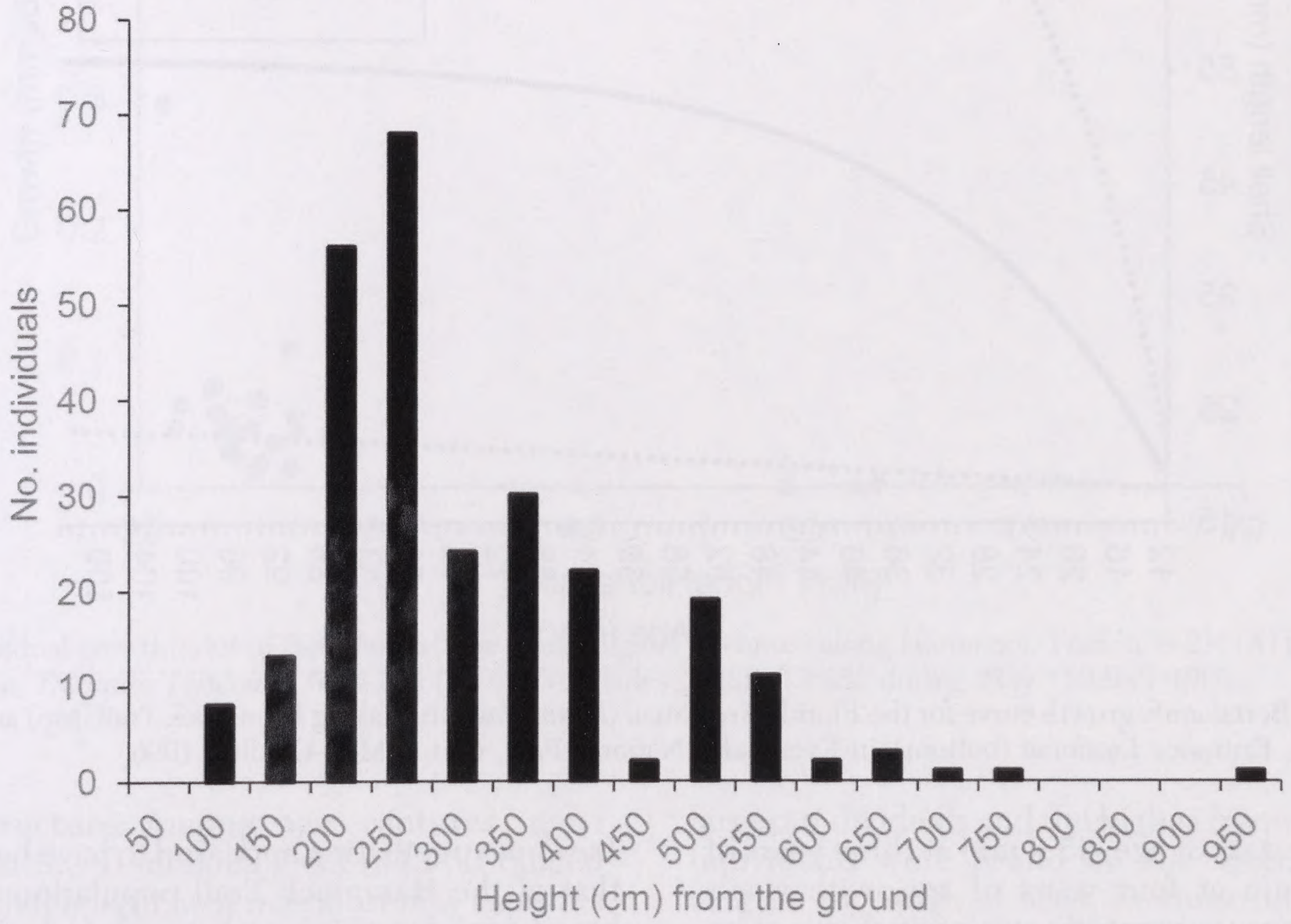
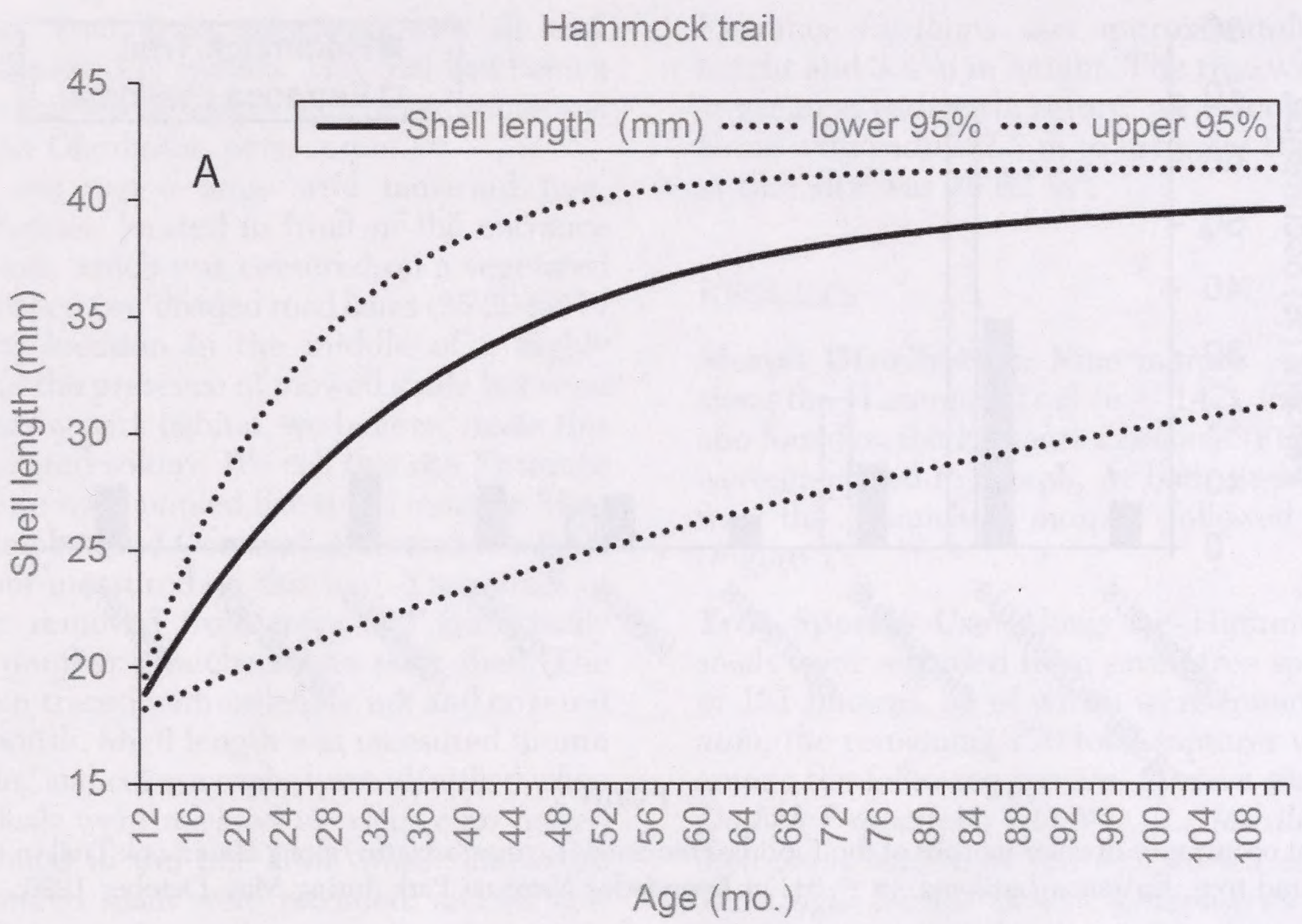


Figure 2. Sampling height distribution of all captures of the Florida Tree Snail (*Liguus fasciatus*) along Hammock Trail (n = 261) in Everglades National Park during April–October 1996.



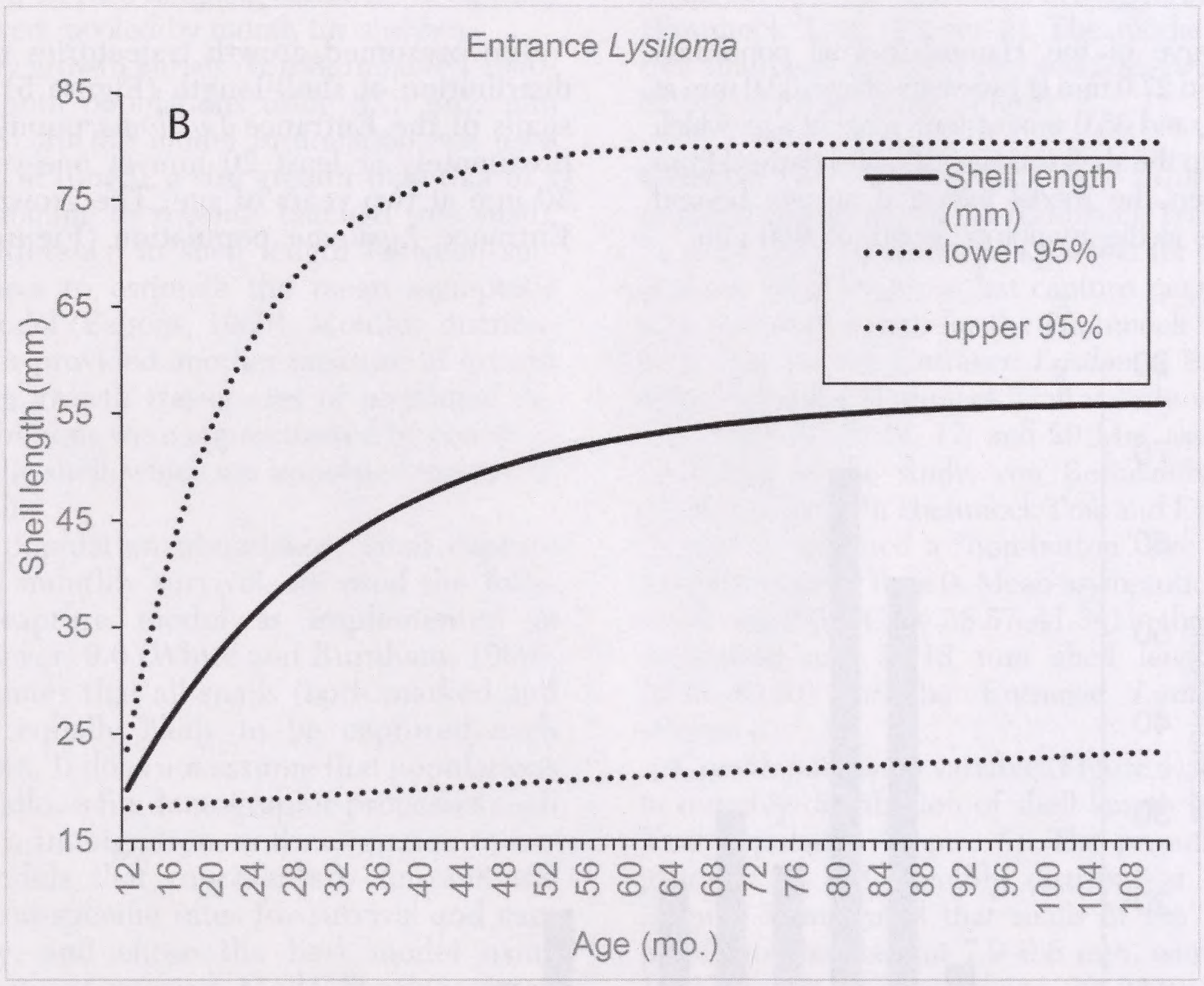


Figure 3. A von Bertalannfy growth curve for the Florida Tree Snail (*Liguus fasciatus*) along Hammock Trail (top) and on an isolated wild tamarind tree, Entrance *Lysiloma* (bottom), in Everglades National Park, during May–October 1996.

36.0 mm at two years of age, 45.0 mm at three years of age, and 50.0 mm at four years of age, with snails reaching their mean asymptotic size of 56.2 mm at an age beyond 111 mo. Growth rate of the Entrance *Lysiloma* population appeared to have been faster than that of the Hammock Trail population; however, the broad confidence intervals associated with each curve preclude a definitive assessment.

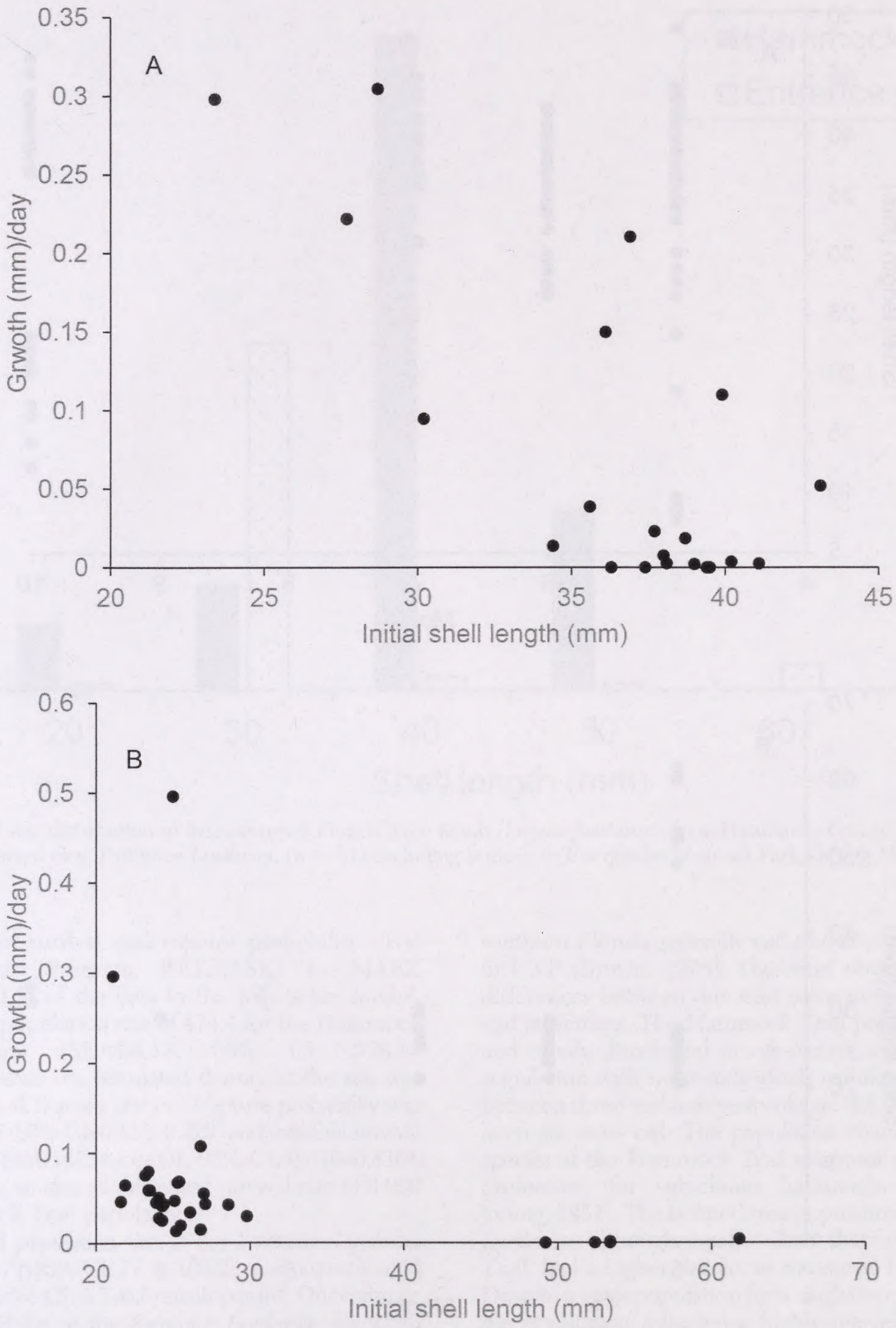


Figure 4. Individual growth rates of the Florida Tree Snail (*Liguus fasciatus*) along Hammock Trail (n = 21) (A) and on an isolated wild tamarind tree, Entrance *Lysiloma*, (n = 31) (B) in Everglades National Park, during May–October 1996.

Population Structure: Among new captures, most tree snails from the Hammock Trail (64.9%) ranged 31–40 mm in shell length, whereas most new captures from the Entrance *Lysiloma* population (85.3%) ranged 21–30 mm in shell length (Figure 6). The largest individuals and the higher frequency of smaller individuals were found on the Entrance *Lysiloma* (Figure 6). Snails at least 40 mm comprised a larger proportion of first captures at the Hammock Trail (17.9%) than on the Entrance *Lysiloma* (1.6%).

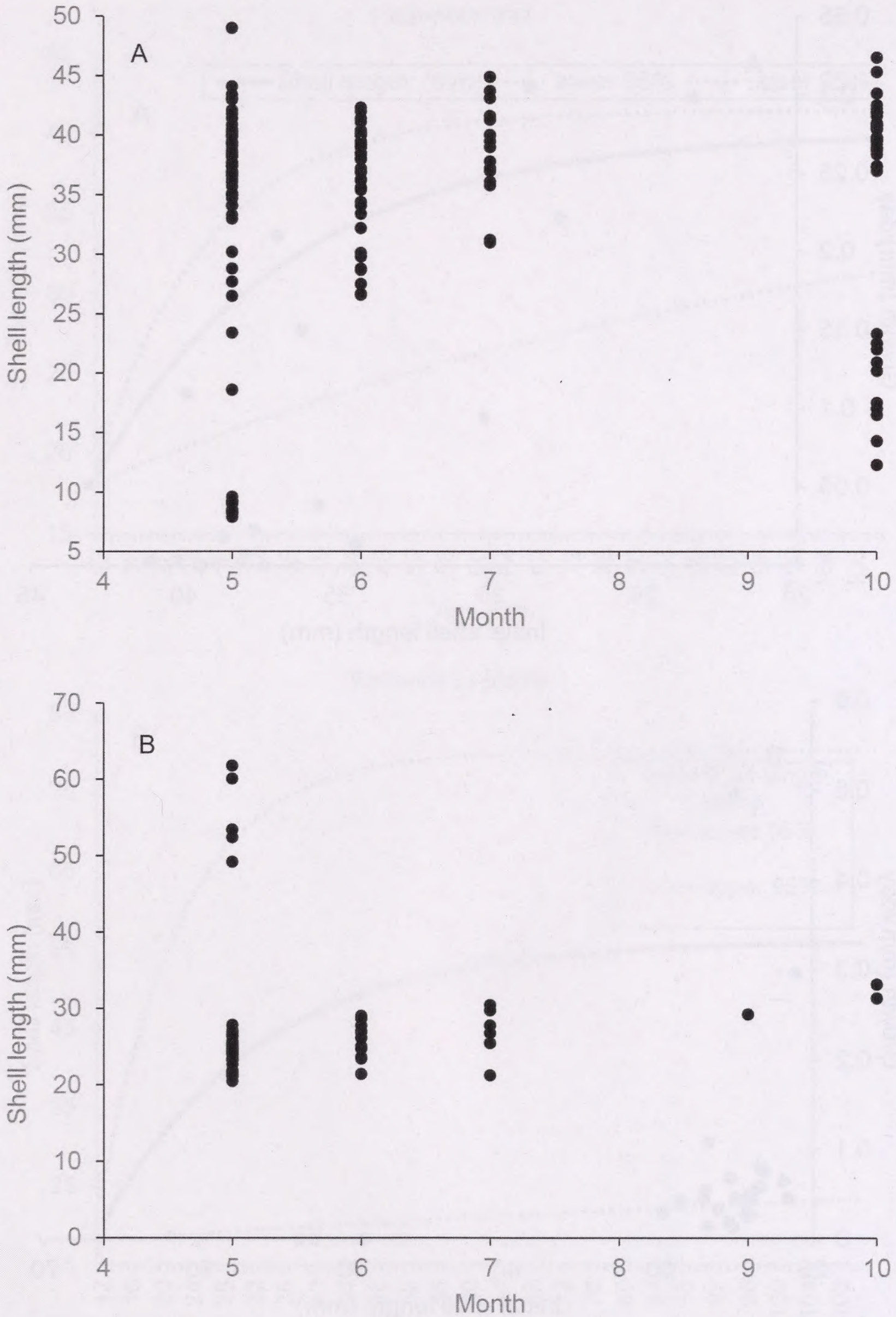


Figure 5. Monthly distribution of shell sizes of the Florida Tree Snail (*Liguus fasciatus*) using first-captures and buttons along Hammock Trail (n = 164) (A) and on an isolated wild tamarind tree, Entrance *Lysiloma*, (n = 61) (B) in Everglades National Park, during May–October 1996.

Age Distribution: Age structure of tree snails varied between sites, most notably in the frequency of very young individuals (Figure 7). Among first captures, snail age at the Hammock Trail was bell-shaped in distribution and one-year-old snails comprised 0.9% of the that sample. At the Entrance *Lysiloma*, the age structure was skewed toward very young snails with one-year-old snails comprising 89.8% of all individuals on the tree and remaining snails being mature.

Population size and Survival: The results of the Jolly-Seber model indicated that the best model at both sites

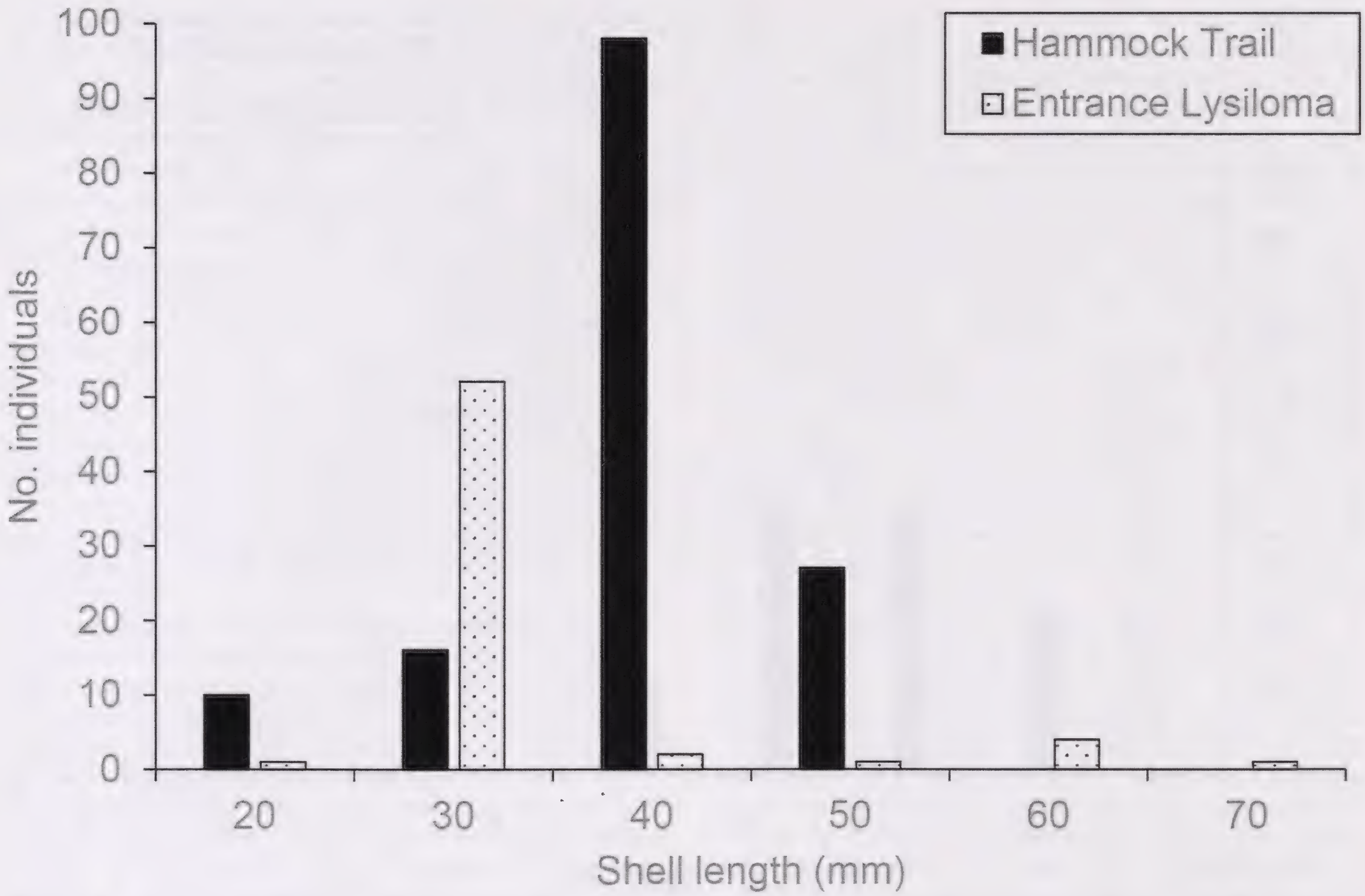


Figure 6. Shell size distribution of first-captured Florida Tree Snails (*Liguus fasciatus*) along Hammock Trail (n = 151) and on an isolated wild tamarind tree, Entrance *Lysiloma*, (n = 61) excluding buttons in Everglades National Park, during May–October 1996.

included constant survival and capture probability. The model fit test (Program RELEASE) in MARK indicated a good fit of the data to the Jolly-Seber model. We estimated a population size of 474.4 for the Hammock Trail population (SE=58.13, 95% CI: 378.9–609.5), which means our estimated density at the site was 4.7 (95% CI: 3.8–6.1) snails per m^2. Capture probability was 0.168 (SE=0.027, 95% CI: 0.121–0.229) and monthly survival probability was 0.810 (SE=<0.001, 95% CI: 0.810–0.810), which represents an annual estimated survival rate of 0.080 for the Hammock Trail population.

The estimated population size at the Entrance *Lysiloma* was 89.5 (SE=7.77, 95% CI: 77. 9–109.2), thus our estimated density was 5.4 (95% CI: 4.7–6.6) snails per m^2. Our estimate of capture probability at the Entrance *Lysiloma* was 0.545 (SE=0.067, 95% CI: 0.413–0.670) and monthly survival probability was 0.759 (SE=0.045, 95% CI: 0.660–0.835), which represents an annual estimated survival rate of 0.036.

DISCUSSION

The two populations of Florida Tree Snails of our study differed in several respects from one another; however, other traits of these populations conformed to those of southern Florida generally and to those studied elsewhere in ENP (Brown, 1978). The most obvious demographic differences between our sites were in population density and structures. The Hammock Trail population was large and evenly distributed in age-classes, essentially a stable population with most individuals estimated to have been between three and four years of age, the oldest snail having been six years old. The population characteristics of this species at the Hammock Trail were not unusual given its preference for sub-climax hammocks (Brown, 1978; Young, 1951). The isolated tree population of the Entrance *Lysiloma*, although smaller than that of the Hammock Trail, had a higher density as measured by no. snails/ m^2. Despite a large population for a single tree, the structure of the population reflected a highly uneven distribution of snails, such that an age gap separated a population composed of mostly of yearlings from a few adults. The absence of two-year-old snails and the dearth of snails at the end of their second season of life indicate that Entrance *Lysiloma* had a small but highly dense resident population comprising mature and some very old adults approximating the maximum lifespans of eight and nine years of age known for the species (Doe, 1937; Jones, 1954).

The estimated abundance of an intensively studied population of Florida Tree Snails in a Long Pine Key

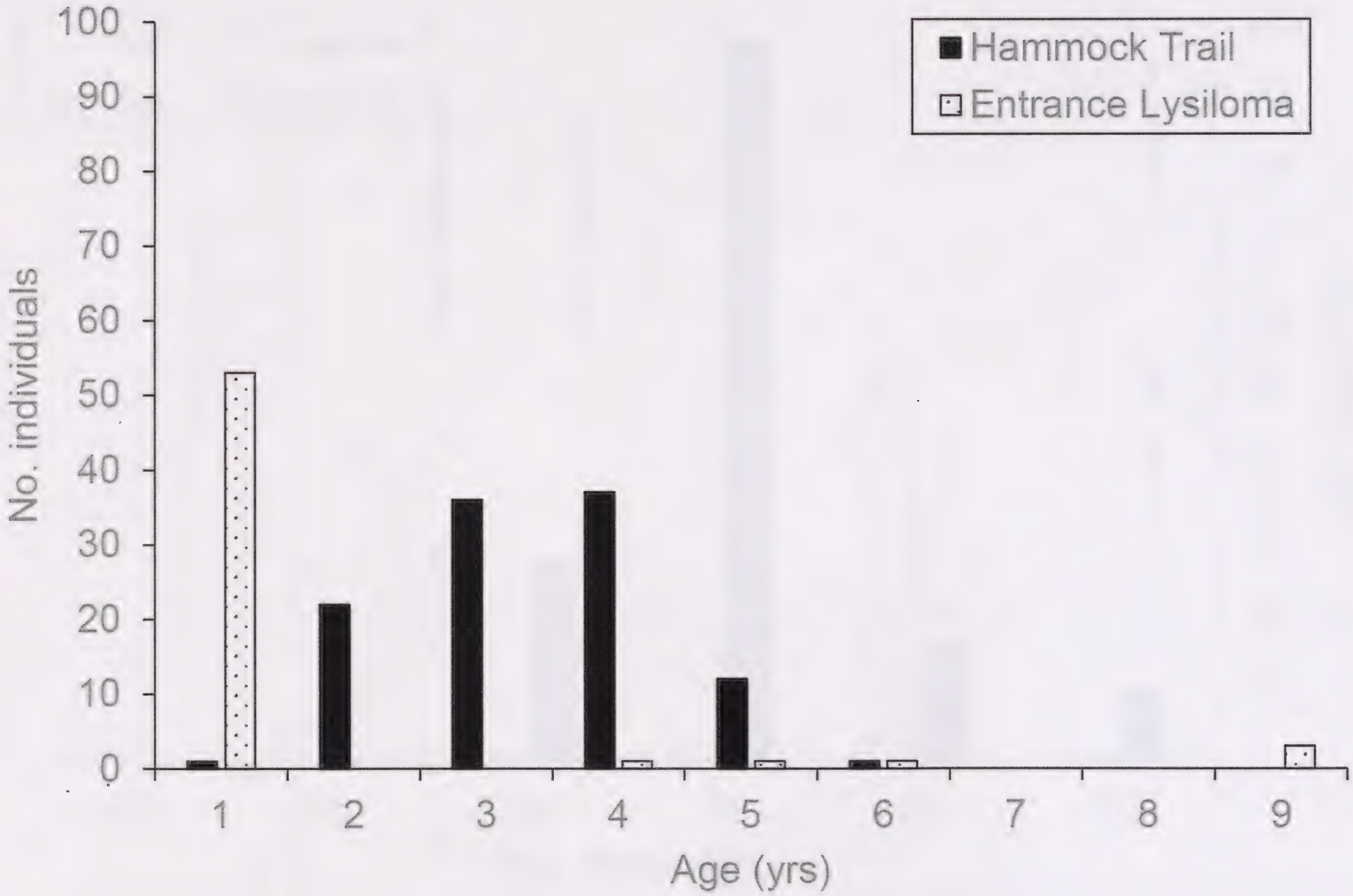


Figure 7. Age distribution of the Florida Tree Snail (*Liguus fasciatus*) along Hammock Trail (n = 109) and on an isolated wild tamarind tree, Entrance *Lysiloma,* (n = 59) in Everglades National Park, during May–October 1996.

hammock of ENP (Brown, 1978) ranged from 1,177 individuals (Bailey Modified Lincoln estimate) to 1,269 individuals (Lincoln estimate), and one-year-old snails comprised 54.2 and 57.1% of the total population by each estimation, respectively. Subsequent age-classes were much smaller in number, the highest of which were two- and three-year-old snails. Very few snails reached the age of seven years (Brown, 1978). A comparison among our populations and Brown's (1978) revealed similarity of Brown's (1978) population with Entrance *Lysiloma* but with much more recruitment. To that end, annualized survival rates were twice as high among snails along the Hammock Trail (8%) than on the Entrance *Lysiloma* (4%) where a severe bottleneck existed in young age-classes. Brown (1978) found lower survivorship among two-year-old snails than three-year-old snails.

A plausible alternate hypothesis to explain the heavily skewed population structure of the Entrance *Lysiloma* is based upon recent colonization. In this scenario, at least six founders (49.2–61.8 mm) colonized the tree, and the flush of one-year-old snails could represent the first reproduction of the colony. However, the shell sizes of the founders were large and, more importantly, their ages, based on resting line counts, ranged from four to nine years of age. Thus, it may be more likely that reproduction had occurred on the Entrance *Lysiloma* more than once by those founders. If this scenario is true, then the largest size- and age-classes represent original founders, and the smaller and younger adults are either also original founders that colonized the tree when young, recent colonizers, or results of successful recruitment on a tree that does not seem capable of sustaining many adults. This hypothesis is not necessarily in conflict with our suggestion of resource limitation as an explanation of the skewed population structure if colonization of the lone tree had occurred earlier as we suspect. Regardless of timing, Entrance *Lysiloma* presented an ideal colonization start for Florida Tree Snails as a large and preferred tree species in a sunny area, and the morph frequency of its snails reflected that of primary colonizers. All adults on Entrance *Lysiloma* were *castaneozonatus*, and all but one individual, a juvenile, were *castaneozonatus, cingulatus,* and *luteus*: *cingulatus* was found to disperse a lot (Brown, 1978), and *castaneozonatus* and *cingulatus* were reported as first colonists of small young hammocks (Simpson, 1929).

If density-dependence drove the different population structures at our two sites, it may also have affected the maximum body and age sizes between them. Humes (1965) reported bigger snails after a fire, and Brown

(1978) found more and larger snails in sunny areas. Perhaps the isolated nature of the Entrance *Lysiloma* mimicked the effects of a fire, providing a few snails with enough food to grow old quickly but not enough food to sustain a growing population.

Between our study sites, growth curves also were suggestive of a faster growth rate at Entrance *Lysiloma*. However, the the wide confidence intervals preclude any confirmation that apparent intersite differences in growth curves reflected actual differences in growth rates.

The rate of first year growth was similar among studies. Hatchling (button) size is 7 mm (Weber, 1953; Voss, 1976), and Brown (1978) determined that buttons grew 2.2 mm/ mo. At Hammock Trail, buttons having reached 17.0 mm by October would have grown 2.0 mm/ mo. Those of Entrance *Lysiloma* having reached 20 mm would have grown 2.6 mm/ mo. unless smaller individuals had been missed in May. Voss's (1976) finding of 10 mm would be reduced to growth rate the first 2.0 mm/ mo. during May–October.

Comparatively, age and size-class relationships from Hammock Trail were similar to those reported by Brown (1978), who likewise found rapid growth at ages one through four years of age. Brown (1978) also detected no significant differences in shell length among snails four to six years of age with no real growth after five years of age. Simpson (1920) also noted rapid growth during the first two years but also noted slower growth during ages three and four. Age at maturity was in general agreement among studies. If maturity is achieved at 40 mm, some could reach maturity at three years of age (Brown, 1978; this study), and all mature at four years of age (Brown, 1978; Solem, 1961; Voss, 1976; this study). To that end, the range of shell size among the smallest cohort at Hammock Trail in October underscores the potential for variation in hatching time and in individual growth rate. We also note that despite overall similarity in growth rates among studies, it is important to recognize that year to year variation in food quality can differentially affect growth rates of one or more segments of the population.

The Long Pine Key region of ENP is inhabited by resident and transplanted forms of Florida Tree Snails (Jones et al., 1981). *Castaneozonatus* and *cingulatus* were the dominant morphs at both of our sites. With nine morphs, Hammock Trail had more than twice the number of morphs than Entrance *Lysiloma*, and the morphs on the Entrance *Lysiloma* were a subset of those on Hammock Trail. *Castaneozonatus* was clearly the dominant morph at both study sites, whereas *cingulatus* was less prominent at the Hammock Trail than on the Entrance *Lysiloma*. Seven morphs were represented in Brown's (1978) site on Long Pine Key, and *castaneus* (47.3%) and *castaneozonatus* (44.1%) were similarly dominant.

Features of a hammock influence morph distribution. Larger hammocks are associated with greater morph diversity (Rex, 1972), and darker forms are more common in the center of the hammock while lighter morphs typify hammock edges (Brown, 1978; Roads, 1899; Pilsbury, 1912). Having surveyed along a partially sunny transect at Hammock Trail, we do not know how reflective the morph frequencies were for that of the entire hammock. The two most frequently encountered morphs at both sites of our study, *castaneozonatus* and *cingulatus*, are associated with colonizing abilities (Brown, 1978; Simpson, 1929). Consequently, the morph frequencies of Hammock Trail, were likely accurate, having reflected a young less canopied hammock but more developed than the perennially incipient hammock of Entrance *Lysiloma*.

We do not know the frequency of host tree species along the Hammock Trail; however, snails were numerous at that site and were found primarily on *L. latisiliquum* and *Sideroxylon salicifolium*. Combined, these two species comprised 84.1% of non-button tree snail sightings. Association of tree snails with these two species, and especially of *L. latisiliquum*, would be higher yet if 131 buttons, all of which were detected on *L. latisiliquum*, were included in the analysis. Our findings of tree use by Florida Tree Snails and their buttons conform to findings of host tree preferences from other studies. Whereas *Piscidia piscipula* was found to be the preferred tree of tree snails on the Florida Keys, *L. latisiliquum* was preferred on the mainland (Pilsbury, 1912). *Lysiloma latisiliquum* was found to have been favored by buttons (Brown, 1978). On LPK, tree snails favored *L. latisiliquum* but also *M. toxiferum* and *S. salicifolium* (Brown, 1978). In Big Cypress National Preserve, tree snails differentially occupied *L. latisiliquum* and to some extent *Zanthoxylum fagara*, and snails were less likely to leave a *L. latisiliquum* or large tree (Bennets et al., 2000).

An interesting finding by Brown (1978) was that Florida Tree Snails differentially used the sunniest areas of the hammock. Because we did not measure this variable, we do not know the extent to which sunshine was a limiting resource or if their tree height distribution was related to sunlight to that or some other variable. We are confident, however, that even to 550 cm, we could detect tree snails, which indicates the actual tree height preference during those times of day and year that we surveyed them. If so, we cannot rule out that morning or afternoon light could have provided the direct light sought by these tree snails.

Many aspects of Florida Tree Snail ecology of our sites conformed to ecological traits of the species. The most significant difference between our sites was the population structure. Body size distribution was bell-shaped, and age structure reflected a stable population along the Hammock Trail. The population structure and growth curve of the Entrance *Lysiloma* appeared to be consistent with a demographic response to a strongly limited food resource. Consequently, a small population of large and older snails resided on a single tree that was seasonally and ephemerally populated with progeny, most of which were gone by the end of the season; a population perhaps stuck at an early colonization stage. Yet, a tree such as the Entrance *Lysiloma* in an incipient hammock could in turn serve as a nursery critical to the establishment of a colony; in this case overwhelmingly by the three known colonizing morphs of the four morphs present.

ACKNOWLEDGEMENTS

This study is dedicated to the memory of Archie Jones, a gentleman whose knowledge of Florida Tree Snails will be missed. Work on this project was conducted when WEM was employed by the National Park Service at ENP as Supervisory Curator for the four south Florida national parks. Thanks are due to Carl McCarty for his work on this project and to Lori Oberhofer, wildlife biologist at Everglades National Park, for information regarding location of the now non-existent Hammock Trail site of our study.

LITERATURE CITED

Bennetts, R.E., S.A. Sparks, and D. Jansen. 2000a. Host-tree selection by Florida tree snails, *Liguus fasciatus* (Müeller, 1774), in Big Cypress National Preserve, Florida, USA. The Nautilus 114: 112–116.

Bennetts, R.W., S.A. Sparks, and D. Jansen. 2000b. Factors influencing probabilities of Florida tree snails *Liguus fasciatus* (Müller) in Big Cypress National Preserve following Hurricane Andrew. Malacologia 42: 31–37.

Brown, C.A. 1978. Demography, dispersal, and microdistribution of a population of the Florida tree snail, *Liguus fasciatus*. Unpublished MS Thesis. University of Florida, Gainesville, FL. 134 pp.

Diamond, J.M. and J.T. Heinen. 2016. Conserving rare plants in locally-protected urban forest fragments: A case study from Miami-Dade County, Florida Urban Forestry and Urban Greening 20: 1–11.

Doe, M.F. 1937. Tree snails of south Florida. Nature Magazine 29: 82–84.

Fabens, A.J. 1965. Properties and fitting of the von Bertalanffy growth curve. Growth 29: 265–289.

Hillis, D.M., M.T. Dixon, and A.L. Jones. 1991. Minimal genetic variation in a morphologically diverse specie (Florida tree snail, *Liguus fasciatus*). Journal of Heredity 82: 282–286.

Humes, R.H. 1965. A short history of *Liguus* collecting with a list of collectors 1744–1958. Tequesta 25: 67–82.

Jones, A.L. 1954. How Florida tree snails live. Everglades Natural History Magazine 2: 59–62.

Jones, A.L., E.C. Winte, and O.L. Bass, Jr. 1981. The status of Florida tree snails *Liguus fasciatus*), introduced into Everglades National Park. South Florida Research Center Report T-622, 31 pp.

Pilsbry, H.A. 1912. A study of the variation and zoogeography of *Liguus* in Florida. Journal of the Academy of Natural Sciences of Philadelphia 15: 429–471.

Pilsbry, H.A. 1946. Land Mollusca of North America (north of Mexico). Academy of Natural Sciences of Philadelphia Monograph 3(2) part 1 of 2: 37–102.

Rex, M.A. 1972. The relationship of island area and isolation to color polymorphism in *Liguus fasciatus* (Pulmonata, Bulimulidae). Breviora 391: 1–15.

Roads, I.N. 1899. Annotated list of land and fresh-water shells recently collected in the vicinity of Miami, Florida. The Nautilus 13: 43–48.

SAS Institute. 1988. SAS/STAT user's guide. Release 6.03 edition. SAS Institute, Cary, North Carolina, USA.

Simpson, C.T. 1920. In lower Florida wilds. G.P. Putnam's Sons, New York, 393 pp.

Simpson, C.T. 1929. The Florida tree snails of the genus *Liguus*. Proceedings of the United States National Museum 73: 1–44.

Solem, A. 1961. Gems of the Everglades. Bulletin of the Chicago Natural History Museum 32: 8–9.

Von Bertalanffy, L. 1960. Principles and theory of growth. Pages 237–259 in: W.W. Nowinski (ed.) Fundamental aspects of normal and malignant growth. Elsevier Sci. Publ., Amsterdam, The Netherlands.

Voss, R.S. 1976. Observations on the ecology of the Florida Tree Snail *Liguus fasciatus* (Müeller). The Nautilus 90: 65–69.

Weber, J.A. 1953. Nests of the Florida tree snail. Everglades Natural History Magazine 1: 63–65.

White, G.C. and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 (Supplement): S120–139.

Young, F.N. 1951. Vanishing and extinct colonies of tree snails, *Liguus fasciatus*, in the vicinity of Miami, Florida. Occasional Papers of the Museum of Zoology University of Michigan 53: 1–21.

Richard Irwin Johnson (1925–2020), a life well lived

Alan R. Kabat
Museum of Comparative Zoology[1]
Harvard University
Cambridge, MA 02138 USA
alankabat@aol.com

ABSTRACT

This paper discusses the life and works of Richard Irwin Johnson (1925–2020), who made significant contributions to our knowledge of the Unionidae (Mollusca: Bivalvia) through his numerous publications and his curation of the sizable collections of freshwater bivalves at the Museum of Comparative Zoology, Harvard University. Johnson also published extensively on the history of malacology, including biographical accounts and museum histories. His 135 publications on mollusks spanned 74 years (from 1941 at age 16 to 2015 at age 90), nearly setting a record for malacology, and his membership in the American Malacological Union / Society for 79 years (1941 to 2020) outlasted any other current or former member. Johnson amassed one of the largest ever private libraries of books and journals on mollusks, and contributed significantly to the growth of the MCZ Malacology Library.

Additional Keywords: Unionidae, Museum of Comparative Zoology, Harvard, American Malacological Union

INTRODUCTION AND SOURCES

This biography is based upon: (1) reviewing Johnson's 74 years' of publications; (2) correspondence with his colleagues; (3) my friendship of over 35 years with him; (4) two prior biographical articles (Boss, 1998; Reed, 1998); (5) his publications on the study of mollusks at Harvard; (6) his autobiographical account of his World War II service (2007);[2] and (7) the quite informative "class notes" that he submitted for his Harvard College Class of 1951's alumni reports, which appeared every five years from 1961 through 2016 (except for 1981) (1961, 1966, 1971b, 1976b, 1986, 1991a, 1996a, 2001, 2006a, 2011, 2016). These alumni reports, colloquially known as the "Red Books," are an invaluable biographical reference on Harvard undergraduates (Atlas, 2012). While most of his classmates submitted staid descriptions of their career progression, Johnson was almost unique in using his submissions as a vehicle for making humorous and ironic comments on his own work and for discussing his wide-ranging interests.

Early Years and Malacological Beginnings

Johnson was born on March 17, 1925, the oldest child of Karl Hilmer Johnson (1896–1985) and Louise Irwin Johnson (1898–1981); his sister Margery (born 1928) soon joined the family, and survives him. Johnson passed away, at home, on July 1, 2020.

His father, Karl ("Pike") Johnson, as a high school student in Everett (Massachusetts), was on the high-school football team that achieved the highest-ever scores in Massachusetts (2007: 220). Pike Johnson later played in the very first professional football season in 1920, as part of the "Akron Pros," which went on to win the first-ever national championship at the predecessor to the NFL's Super Bowl (Pennington, 2020).

Johnson and others have often told the story of how he became interested in mollusks, and ended up devoting a lifetime to the Unionidae, the highly diverse and difficult to study family of freshwater clams or bivalves (2006h: 133; Boss, 1998: iii; Reed, 1998: 107). In 1939, his high-school science teacher, Albert Clish, took Johnson and a fellow student, Allen Crocker, to meet Clish's former classmate, William James Clench (1897–1984), then the longtime Curator of Mollusks at Harvard's Museum of Comparative Zoology (MCZ). Clench made quite an impression on the two teenagers, who then spent their Saturdays volunteering in the Mollusk Department:

> "As in past years, much of our continued growth, particularly in the conditioning of our material, is due to several young men who act as volunteer workers in the department. This year, Mr. A. C. Crocker and Mr. R.I. Johnson have spent nearly every Saturday doing many tasks of labelling, sorting and distributing material in the collection. . . . To these young men I am exceedingly grateful for their interest and for their willingness to do the tasks set before them." (Clench, 1940: 31).

Ironically, Allen Crocker (1925–2011), who became a distinguished physician, instead remarked, years later,

[1] Research Associate
[2] Citations to Johnson's own papers are indicated simply by the year, in parentheses. If more than one paper was published in the same year, then letters are used to specify each paper in that year.

that "My first choice was entomology... I thought insects were cool" (Marquard, 2011). Johnson, however, persevered with mollusks, specifically the Unionidae, for the rest of his high school years, so much so that his high school yearbook, under "Ambition," listed "Malacologist" (Anonymous, 1942: 56). Although Johnson's first two papers were short notes in *The Nautilus* on finding freshwater snails in new localities in Massachusetts (1941) and Vermont (1945), his remaining scientific publications were primarily on the Unionidae.

American Malacological Union / Society

Clench also got Johnson involved in the then-new American Malacological Union (now the American Malacological Society), the scientific organization founded in 1931 by Clench, Henry Pilsbry (1862–1957, curator at the Academy of Natural Sciences of Philadelphia) and Norman Lermond (1861–1944, an eccentric researcher in Maine). Although Johnson formally joined the AMU in 1941, he first attended its annual summer conference in June 1940, at the Academy of Natural Sciences. After the banquet dinner at the end of that conference, Clench tasked Johnson with walking Pilsbry (who was 78 years old) to Philadelphia's 30th Street train station so that Pilsbry could take the commuter train to his suburban residence. About halfway there, Pilsbry, who ate and drank too much that evening, unexpectedly threw up on the sidewalk. Johnson, speechless and too young (age 15) to have experienced alcohol, continued walking with Pilsbry. After another block, Pilsbry grabbed Johnson's elbow, and dragged him back to the site, whereupon Pilsbry, with his bare hands, reached into the vomit, retrieved his false teeth that had fallen out, put the false teeth back into his mouth, and the duo then continued back to the train station. Johnson was later to remark that he would never be able to forget this scene.

Nonetheless, Johnson did return in August 1941 to the next annual conference, held in Thomaston and Rockland, Maine, where he was able to meet yet other senior names of malacology, including Lermond and Frank Collins Baker (1867–1942) (Boss, 1998: iv). Johnson later presented several papers at the annual conferences (1947a, 1955, 1956a, 1958, 1960, 1962) and also served on the AMU's Council for a two-year term in the 1960s. Johnson became a life member of the AMU/AMS, and at the time of his death, was both the oldest and the longest serving member of the AMS. The oldest current member of the AMS appears to be John (Jack) Burch (born in 1929, and joined AMU as a graduate student in 1954), with Alan Kohn (born in 1931 and joined AMU as a graduate student in 1955) close behind, while the longest serving member of the AMS is now Barry Roth (joined AMU in 1951, at the age of 9).

Boston Malacological Club

Johnson also participated in the Boston Malacological Club (BMC), the second-oldest malacological society in the U.S.A., founded in 1910 (Figure 2). He served as President from 1955 to 1957, and presented several talks that reflected his interests in book collecting:

(1) May 1951, "History of early books on shells" (Farrell, 1952);
(2) November 1952, "American conchologists and their books" (Farrell, 1954);
(3) January 1954 (?), "Display of rare books on conchology" (Carlson, 1955);
(4) January 1956, "Thomas Say and the New Harmony Movement" (Culligan, 1957);
(5) February 1959, "Conchologists of the American exploring expeditions" (McCallum, 1960); and
(6) October 1962 (?), "Collecting fresh water mollusks in Florida" (Crowley, 1963).

George Buckley, who as a teenager started attending the BMC meetings and volunteering at the MCZ, got to know Johnson early on:

> "He was indeed a character of the highest order . . . boisterous, opinionated, erudite, detailed in all regards, always very bespoke of habit – no one wore a tuxedo better than he did; a rare book collector and expert who donated much of the MCZ Mollusk Department's superb malacology library and was a major collector and researcher of freshwater clams who single-handedly built the superb Harvard Mollusk Department's freshwater clam collection and its then-separate *Unio* room!" (G. Buckley, in litt., 2 Aug. 2020).

Johnson was instrumental in encouraging local enthusiasts to join the BMC, including George Buckley and Kristina Joyce, who remain members, decades later (Buckley, 2020).

World War II

In December 1941, while Johnson was a senior in high school, he accompanied Ruth Turner (1914–2000), who then worked at the Boston Society of Natural History and later became a curator and professor at the MCZ, and James Miller (a professional collector) on a trip to Rhode Island to collect starfish for a biological supply house. Turner left the trip a day early to participate in the Audubon Society's annual bird count; when Johnson and Miller returned to port on 7 December 1941, they learned that Pearl Harbor was bombed earlier that day (2006h: 135–137).

Johnson was drafted into the U.S. Army in June of 1943, at age 18, one year after graduating from high school. This put an end to his work at the MCZ, as Clench recognized in his annual report for 1942–43: "Mr. Richard I. Johnson, an enthusiastic volunteer worker, has entered the Army but before he left had made great improvement in our very large collection of Unionidae" (Clench, 1943: 15). Initially, Johnson was sent to Camp Devens in northern Massachusetts, where he found (in the military library) and read the 1924 translation of Alfred Wegener's *The*

Figure 1–4. **1.** Johnson, World War II veteran and Harvard freshman (1947) (originally published in Maynard, 1948: 106). **2.** William J. Clench and Johnson, Boston Malacological Club picnic at Rye, New Hampshire (1951) (courtesy Boston Malacological Club). **3.** Johnson at the Biological Laboratories (Harvard), with one of Katharine Ward Lane's *Rhinoceros* sculptures (1990s) (courtesy MCZ Malacology Department; copied by Dan Graf) (Ambler, 1973; Bunting, 1985: 170–171, 307). **4.** Johnson in the MCZ "*Unio* Room" (1998) (originally published in Reed, 1998: 106) (© Stu Rosner and reprinted with permission).

Origin of Continents and Oceans, "which had a profound influence on my concept of the distribution of plants and animals before plate tectonics was accepted" (2007: 220) (notably, several MCZ curators, including entomologist Philip Darlington and paleontologist Bernhard Kummel, were reluctant to accept plate tectonics until the 1960s).

Johnson then went to Camp Hood (Texas) for thirteen weeks of basic training as a Private (the lowest rank). It was there that Clench sent Johnson the page proofs for his first major paper, the biography of J.P. Couthouy (due to wartime paper rationing, this was not published until 1946); as Johnson frequently recounted, he read the page proofs while on latrine duty (2007: 220). Once basic training was completed, his group transferred to Iowa State College for further training in the Army Specialized Training Program, but the U.S. Army, without explanation, instead decided that his group would go on combat duty, so they were sent to Fort Leonard Wood in Missouri as part of the 97th Infantry Division scheduled for active combat in late 1944. Unexpectedly, the day before Johnson was to be shipped to Europe for combat duty, he fell out of a Jeep, was unconscious for several days, and missed combat duty entirely (2007: 221).

Eventually, Johnson was shipped to Europe in early 1945, and his first assignment was "with a graves registration outfit at Sainte Mère-Église," the first French town liberated by the Allies, where his duty was "trying to identify bodies that had already been in the ground for a year . . . . This was not especially pleasant work, but a cigar made it easier" (2007: 221). He was transferred to Le Havre, handling quartermaster duties (supply chain logistics, in modern parlance) where he "was occasionally able to sneak to [liberated] Paris on weekends . . . where I bought almost every rare book I could find on conchology, since I already knew the literature" (2007: 221).

Johnson then transferred to Giessen (Hesse, Germany), which had just been conquered, and then to Frankfurt-am-Main, also newly conquered, where his duties were overseeing a warehouse of vegetables. Johnson was able to spend his weekends visiting Munich, Heidelberg, Wiesbaden, and elsewhere, and bought malacological books which he then shipped home for his own use or to resell. Johnson even sent a fellow soldier to Berlin, by Jeep through the Soviet Sector (which later became East Germany), to buy multiple sets of Thiele's *Handbuch der Systematischen Weichtierkunde* (1929–1935), which Johnson then re-sold to a number of American malacologists and libraries, as that important malacological treatise was then quite rare in the U.S.A. Johnson also returned to Paris for a weekend in order to buy a newly available complete set of Reeve's *Conchologia Iconica* (20 volumes, 1843–1878), ship it home, and return to Frankfurt, all without his commanding officer noticing his absence (2007: 222).

Harvard College 1947–1951

Johnson was a late-starter at college. Although he was decommissioned in April 1946, the large influx of (male) veterans after the end of World War II resulted in more students ready for enrollment at Harvard than could be accommodated. Also, Johnson inexplicably failed a physics course during Army basic training – he later claimed that this was caused by a defective slide rule (2001: 257–258) – so Harvard required him to take a year of "prep" courses at the New Preparatory School (Cambridge) before enrolling in September 1947, at the age of 22 (Figure 1).

Johnson was unique among his classmates in remaining active in research at the MCZ, and publishing eight papers and one book review while an undergraduate (1947b–1951a), bringing his career total to 12 papers and one book review by the time he graduated. Even today, few undergraduates can claim such a publication record in the scientific literature.

Surprisingly, given his eventual deep knowledge of the systematics and biogeography of the Unionidae, Johnson was not a Zoology major in college. He instead chose to major in the then-new "Social Relations" Department, a combination of sociology, social psychology, and cultural anthropology. He later remarked that the most useful course he took was the "Rare Books" course taught at Houghton Library, Harvard's rare book library (1976b: 489).

Of the 1,270 other members of the Class of 1951, among those who are probably the widely known are the science fiction author Ursula Le Guin (1929–2018); the poets Donald Hall (1928–2018) and Adrienne Rich (1929–2012); and Richard Welch (1929–1975), the CIA Chief of Station in Athens (Greece) whose assassination was a major turning point for the CIA.

While at Harvard, another of Johnson's distinctions was being an "alternate" on the Freshman Crew, the rowing team for the first-year students. As an alternate, he could only participate in the races if one of the eight regular members was ill or otherwise absent. This did happen at the end of the season, and he became the "eighth" member of the crew during the annual Harvard-Yale Regatta in 1948, in which Harvard's freshman crew beat Yale by a mere 8 seconds in a 2-mile race (Anonymous, 1948: 8; Danzig, 1948). Indeed, this was the only race that the Freshman Crew won that season, so Johnson's addition must have made a difference. James Mathewson (Harvard '51), who was the bow (first seat) on that crew, recently remarked: "That was the only race we won, but the result was a 'perfect' season, by definition" (Mathewson, 2020). In 1995, at Johnson's 70th birthday party, William Curwen (Harvard '50), who was the stroke (last seat) on the Varsity Crew (which also beat Yale, but by only 2 seconds in a 4-mile race), explained "what he meant when he said that there were seven oarsmen and Johnson in the freshman boat that beat Yale" (1996a: 84). Mathewson agreed, "Richard was more mature mentally and physically; Curwen was right. The campus characteristics in 1947–48 were heavily influenced by [military] veterans like Richard." (J. Mathewson, in litt. 11 Oct. 2020).

Sixty-five years later, Johnson's daughter Sally gave him the book *The Boys in the Boat*, about the University of Washington crew who won the gold medal for the U.S.A. at the infamous 1936 Berlin Olympics, where they were filmed by Leni Riefenstahl (Brown, 2013). Johnson remarked to me that his initial reaction to this book was "Why would I care about the University of Washington crew?" However, after reading several chapters, he soon realized that the head coach at Harvard (Thomas Bolles) and the freshman coach (Harvey Love), whom he trained under in 1947–1948, were both hired by Harvard in 1937 from the University of Washington, in order for Harvard to rebuild its crew after having badly lost in the trials for the 1936 Olympics (Hunter, 1948: 128–129; Drury, 1964: 607–621). Johnson read the entire book with unexpectedly great enthusiasm and highly recommended it to others. Thus, it was 65 years before Johnson realized that he had trained under the some of the same coaches who took the University of Washington crew to the gold medal in the Berlin Olympics.

Family Life

In early 1954, Johnson became engaged to Marjory Weld Austin (1927–1988); as was then customary in that social circle, both the engagement and the wedding were covered in the national news, including the *New York Times* and the *Washington Post* (Anonymous, 1954a–1954g; Sherman, 1954a, 1954b). Marjory, known as Peggy, was from an old Massachusetts family – her Weld ancestors arrived from England in 1635 (Benton, 2004). Prior to their marriage, Peggy was a secretary in the Foreign Service at the U.S. Embassy in Rome from 1951 to 1953, which led to the Johnsons making multiple trips to Europe over the next two decades. They had three children, Sally (married to David Lurie), Marjory, and Richard (married to Karen O'Leary; two sons, Mason and William) (Benton,

2004: 97, 106, 118–119). They divorced in 1982, and Peggy owned an antique shop in Cataumet (near Woods Hole) before passing away in 1988 at the age of 61 (Anonymous, 1988).

Johnson married Marrian Louise (Geer) Gleason in June 1983. Marrian was the widow of Edward Hollis Gleason (Harvard '50), whom Johnson knew as a student. Johnson's story was that when Hollis became engaged to Marrian in 1951, she was only 17 years old, and he told Hollis that she was too young to get married. Johnson later admitted that when he married Marrian, "thirty years later she did not seem too young for me" (1986: 94–95; Reed, 1998: 108). They remained married until her death in 2014, at the age of 79 (Anonymous, 2014).

124 Chestnut Hill Road

An inseparable part of Johnson's identity was his remarkable home and his magnificent personal library, which anyone who visited him could readily recall, decades later. What those visitors did not realize is that this was the residence of not one but two prolific authors, over a period of nearly one century. This Tudor Revival style mansion was built in 1924–25 by Ben Ames Williams (1889–1953) and Florence Talpey Williams (1889–1970) (Williams, 1962: 95, 97). Ben Ames Williams, now long forgotten, was one of the most prolific contributors of short stories to the *Saturday Evening Post* in the 1920s–1930s, and also authored several dozen novels, all historical fiction with an emphasis on "local color" (Harris, 1977; Wepman, 1999). His novels were among the earliest books to be made into Hollywood "talkies" (motion pictures with sound, as opposed to silent movies), and some of his novels made the best-seller lists in the 1930s and 1940s.

The Johnsons bought 124 Chestnut Hill Road (in Chestnut Hill, a district of Newton, just west of Boston) in 1955 from the widowed Florence Williams, and Johnson lived there continuously for the next 65 years. This mansion was home to Johnson's substantial personal library of books, journals, and reprints on mollusks, which sprawled through four rooms on the main floor and overflowed into the sizable attic. This was a true working library, since Johnson and his colleagues used these works in their research. In addition to innumerable rare books, there were also numerous historical paintings, medieval-style tapestries, an antique coat of armor, antique metalwork, and about ten stained glass windows that were inexplicably discarded by Harvard University when the original Busch-Reisinger Museum building, built in 1914 (Bunting, 1985: 168–169, 306–307), was renovated in the 1960s. As Johnson wrote in 2001:

> "I continue to drink cheap beer and smoke expensive cigars, ensconced in the Florentine austerity of Renaissance tapestries and about a third of the stained glass that once graced the apse of the Germanic Museum … given by the Emperor Wilhelm II (better known after 1914 as just the Kaiser) at the time of its opening. Workmen, instructed to destroy it, rescued the Kaiser's glass and sold the panes" (2001: 258).

Several colleagues have shared their reminiscences of 124 Chestnut Hill Road. Robert Chellis, a fellow member of the Club of Odd Volumes (COV, *infra*), wrote:

> "Some evenings after COV meetings Tom Hansen and I would drive Richard home – and then the *real* evening began – his Tudor home, the tapestries, curiosities everywhere, roaring fire, cigars (for matches, lift the armored foot of the suit of armor); the *Nuremberg Chronicle* [1493] and rare volumes open on a reading table; interesting books flagged as conversation starters; and behind a gilded but distressed Renaissance pulpit, some old Virginia Gentleman [bourbon] and a half ice box of cold Pabst Blue Ribbon. Help yourself. And good, enriched, amusing talk. It was time to be savored" (R. Chellis, in litt., 3 July 2020).

Peter Dance, the British historian of conchology and malacology, was similarly impressed:

> "I also visited him in his home near the MCZ, a neo-Gothic affair, bedecked with flags and heraldic paraphernalia partially obscuring the most amazing library of shell books. Tucker Abbott was with me at the time, and I remember him [Abbott] pretending to spill a cup of tea over a copy of the *Nuremberg Chronicle*. Although this was one of Dick's more outstanding treasures, he did not bat an eyelid!" (S.P. Dance, in litt., 4 July 2020).

Johnson also owned two summer cabins near Wolfeboro, New Hampshire – he named the cabins "Mayerling" and "Astapovo" (1971b: 101; 1986: 95). Mayerling was named after the summer home near Vienna where Rudolf, Crown Prince of Austria, murdered his mistress and committed suicide in 1889 as part of a suicide pact, while Astapovo is the Russian train station where Leo Tolstoy died in 1910. However, far from having morbid interests, these names reflected Johnson's sardonic sense of humor and he enjoyed his time at these cabins.

Rare Book Collecting

Johnson soon gained an appreciation of rare natural history books as a high school student, given his exposure to the (then-small) Mollusk Department library at the MCZ, as well as the rare books that Alexander Agassiz and others had acquired for the MCZ Library. This taste, unusual for high school students then as now, resulted in an unexpected opportunity during World War II, when he was able to acquire rare books cheaply in Paris and Germany, as noted earlier. While still an undergraduate, he used the stock he had acquired during the war years to start up a mail-order book business, operating out of his parents' house in Belmont (a suburb of Boston). Indeed, he was able to finance his summer vacations in Europe through his book sales, and he used those vacations as an opportunity to purchase further books for resale in the U.S.A.

Over the years, Johnson acquired a number of unique works, some of which he was able to write about. For example, in addition to the aforementioned set of Reeve's *Conchologia Iconica* that he purchased in Paris in 1945, he later purchased another set which was the original "pattern set," *i.e.*, the template used by the artists for coloring the copies to be sold to customers (1970b). This pattern set was even more unusual in that the reverse side of many of the plates had the mailing address and old British postage stamps, as each original plate was sent through the Royal Mail to the publisher, without using envelopes! Johnson donated this set to the MCZ Mollusk Department library. Johnson also found what was apparently the only reprint (or offprint) of Thomas Say's 1817 article on "Conchology," published in William Nicholson's first *American Edition of the British Encyclopedia*, a reprint that Say had given to Constantine S. Rafinesque, the eccentric naturalist (1975g).

Johnson and fellow MCZ volunteer Richard Winslow Foster (1920–1964) were able to acquire several significant rare book collections. One was in 1942, when the library of Arthur Fairfield Gray (1855–1944), a long-forgotten conchologist, was purchased by Boston bookseller George Goodspeed for a mere 35 cents per volume (2002c: 139–140). Although the two copies of Say's *American Conchology* (1830s) were quickly sold to others, Johnson and Foster were able to acquire numerous titles for themselves and for the MCZ Mollusks Library, including Conrad's *American Marine Conchology*, Delessert's *Recueil de coquilles décrites par Lamarck*, and other rare books by Haldeman, Bourguignat, Servain, and others (2002c: 140).

Another was in 1948, when Wheldon & Wesley (England) was able to acquire most of the library of E.R. Sykes who had, in turn, managed to acquire the library of Sylvanus Hanley (1819–1889) for practically nothing, as amusingly recounted by Dance (1986: 189–196). What Dance did not realize is that Johnson and Foster were the fortunate buyers of the Hanley / Sykes library (2006h: 137). Unfortunately, they must have missed one of Hanley's own books listed in the sales catalog, the exceedingly rare *Photographic Conchology* (1863), which Johnson, years later, told me was the only one of Hanley's books that he did not own, even though it consisted of 7 plates of freshwater clams (5 of the Unionidae *sensu latu* and 2 of the Cyrenidae) (Coan and Kabat, 2012: 289–290, 294). Indeed, only seven institutions, three in the U.S.A. and four in Europe, are recorded in OCLC World Cat (the largest online database of library catalogs) as having that work.

Although some book collectors are known for their artistic bookplates inserted inside the front cover, Johnson instead inexplicably had a rubber stamp with his name, which he would stamp at the top of the title page of each book. This caused a problem when Tucker Abbott arranged to use Johnson's copy of Swainson's *Exotic Conchology* (1821–1841) for a reprint edition in 1968. Abbott and his publisher failed to note Johnson's name stamped on the title page until after the reprint edition was printed and bound; Abbott then had to have the entire edition redone with a new title page inserted and rebound, at significant expense. Bonhams auction house, in selling Johnson's library after his death, remarked that this stamp on his books was "a quiet tribute to one of the great collections of shell books assembled." (Anonymous, 2020a: 71).

Johnson's library required not one but three auctions, with most of the malacological rare books sold by Bonhams on 21 October 2020 (Anonymous, 2020a), other rare books sold by Bonhams on 11 December 2020 (Anonymous, 2020b), and the remaining books and reprints sold by Litchfield County Auctions on 8 December 2020. For example, in 1958 and 1959, Johnson acquired A.A. Gould's Mollusca text and atlas volumes from the U.S. Exploring Expedition (published in the 1850s) from two book dealers in New York and Chicago, each volume for only $50.00. These two volumes were sold by Bonhams in October 2020 for a bid price of $19,000 ($23,825 with the buyer's premium).

Johnson was also able, in those pre-Internet days, to compile complete sets of the articles on mollusks written by several researchers, which he then had bound for each author, in chronological order, with a biography and bibliography up front. It was valuable for research and curatorial purposes to have the sometimes obscure publications of authors from the 1800s compiled this way, which visitors to the MCZ greatly appreciated. Although they never met, Johnson and the science historian William B. Provine (1942–2015) at Cornell University were kindred spirits when it came to assembling and using reprints of scientific papers. Provine (1986: 3) explained that it was vastly easier to work with the reprints of an author's papers as opposed to the bound journal volumes: "When I write, any paper I may need is easily retrieved and sits on the desk within reach. . . . I find the reprint collection to be the perfect complement to my collection of books and personal papers. With all three, research is a constant pleasure with minimal busy work." Thus, Provine (1986: 4) concluded that a comprehensive reprint collection "is invaluable. Without it, the projects that I undertake would be impossible or far more time-consuming." The same was equally true for Johnson.

Club of Odd Volumes (COV)

An inevitable outgrowth of Johnson's interests in rare books and art history was his becoming a member of the Club of Odd Volumes (COV) in 1992. The COV, founded in 1887 and located on Boston's Beacon Hill, is a private club for book collectors, rare book dealers, and letterpress printers. Several well-known naturalists were past members, including Thomas Barbour (herpetologist and MCZ Director from 1927 to 1946) and Samuel Henshaw (entomologist, and Barbour's predecessor as MCZ Director from 1911 to 1927) (Little, 1987: 120, 127).

The COV is known for its monthly dinners, followed by a talk usually focusing on a topic related to book collecting. Johnson gave the talk at the April 20, 1994 meeting.

According to the Minutes prepared by Richard Marius, the talk was titled *Conchological Illustration: Baroque and a Bit Beyond* (Marius, 1994; Rheault, 2004: 35). After a brief introductory spiel explaining that conchology was the study of shells, Johnson noted that he had "read all six volumes of the memoirs" of Giacomo Casanova (1725–1798), and that "Casanova had written that while in Geneva he met a man who knew the names of a thousand shells. It was, said the great Venetian seducer, the most boring evening he had ever spent" (Marius, 1994: 2). Marius explained that, in contrast, "Mr. Johnson was not boring. He used no script for his presentation but seemed inspired by his slides to talk in the rapid pronouncements of an energetic seer, cannonading us with anecdotes, scientific observations, and various other *obiter dictae* with the copious supply of a well-stocked mind. His wit crackled through the evening, evoking laughter and admiration at almost every sentence, and elevating conchology to both learned seriousness and high comedy" (Marius, 1994: 2–3).

Johnson's COV anecdote about Casanova visiting the boring conchologist in Geneva was republished in the *Harvard Magazine* biography (Reed, 1998: 108). I sent this article to several colleagues in Europe, including Yves Finet, curator of mollusks at the Muséum d'Histoire Naturelle, Genève. Finet responded, after consulting with Jean-Claude Cailliez, an expert on the history of Swiss conchology, that "there is no evidence that Casanova ever came to Geneva…" (Y. Finet, in litt., 11 Dec. 1998). Johnson went back to his multi-volume set of Casanova's memoirs, and found an entire section on Casanova's travels in Switzerland (including a stay in Geneva), but realized that the boring conchologist actually lived in Bern, not Geneva. I then looked up Casanova references in Harvard's Widener Library, and discovered that there was, in fact, a scholarly society devoted to Casanova studies located near Geneva, which published a journal, and I reported all this to Finet. Finet and Cailliez regrouped, contacted their neighboring Casanovians, and with the assistance of Ted Baer, another Swiss conchologist, determined that the conchologist in question was Daniel Sprüngli (1721–1801) (Baer, 1999). Finet also published a note on this discovery, coauthored with the editor of the Casanovian journal (Finet and Watzlawick, 1999). Thus, Johnson's stray after-dinner remark at the COV resulted in finally identifying, over two centuries later, the mystery conchologist in Casanova's memoirs.

Thomas Hansen, who was selected to the COV in the same year as Johnson, recalled their subsequent friendship centered around fine books and conversation:

> "As we progressed through – as he put it – 'cheap beer and expensive cigars,' our overstimulated conversation roamed through areas of art and life with great animation and some expertise…. Richard enjoyed talking about his current reading but after that, his own autobiography deserved the most attention. I was fascinated by tales of how he found books in the shells of bombed-out German houses in the mid-1940s. . . . I found amusing Richard's quirky technique of disarming or teasing a conversational partner. . . . This sort of thing was part of the repertoire he had perfected with Kenneth Boss, his dear friend of many years, Harvard malacologist, and a fellow member of the COV. Both had subversive, madcap senses of humor. . . . When we were together, the cascade of anecdotes and quips proved that 'present mirth hath present laughter.'" (T. S. Hansen, Aug. 2020).

The COV is also known for its book exhibits, curated by the members, and sometimes featuring a book or manuscript from each member. In the winter of 2013–2014, the exhibit was "My Favorite Things" (Scinto, 2015). Johnson displayed the very first zoological book he purchased, Gould's *Report on the Invertebrata of Massachusetts* (second ed., 1870). Johnson explained in the exhibit catalog that when he was 14, Clench recommended this book, so "I went to one of the many used book stores in Harvard Square at the time and located this copy for which the price was $2.00. Since that was all the money I had and needed carfare home, I was able to secure it for $1.50. Thus began a lifelong interest in mollusks and the building of one of the largest libraries on the subject in private hands." (Scinto, 2015: 24, 26–27).

Johnson and the MCZ

Johnson, being exposed at an early age to the research at the MCZ, soon realized that the curators were woefully underpaid, and unless they had an independent source of funds (such as Barbour), were limited in their ability to travel overseas or acquire a personal library of rare and scarce titles (Boss, 1998: ix; Reed, 1998: 106–107). He thus resolved to work as a volunteer at the MCZ while earning a living in the business world, eventually becoming formally appointed as an unpaid Research Associate. After graduating from Harvard in 1951, and spending one year studying business at the Thunderbird School (then an independent international business school, now part of Arizona State University), he spent a decade working at insurance and investment firms while continuing to do research on the side (as evidenced by his publications in the 1950s), and was able to acquire the funds to retire by the early 1960s and spend full time on his research.

In particular, Johnson used his personal funds to renovate a large room, off the balcony of the MCZ's Great Mammal Hall, for his office, several student offices, and the sizable Unionidae collections (2006h: 141). This space, known as the "*Unio* Room," became his professional home for nearly five decades (Figure 4). Johnson would give directions to first time visitors to the MCZ, "You will find me by the tail of the sperm whale" (Reed, 1998: 106). One visitor aptly described the setting of his museum office:

> "Johnson's office was located behind a steel door in the upstairs gallery in the hall of mammals, just off the right fin of a vast skeleton of a sperm whale, which is suspended below the ceiling and floats above the lower galleries wherein lie the mounted displays of okapis, guanacos,

Figure 5–6. **5.** Ernst Mayr, Johnson, and Kenneth J. Boss, Dedication of the Ernst Mayr Library with portrait of Professor Mayr by Robert Douglas Hunter (1994) (originally published in Boss, 1998: ii, and republished in Kabat and Johnson, 2015: 9). **6.** Edward O. Wilson and Johnson, two long-time MCZ researchers, on the occasion of the dedication of a tree in the MCZ Courtyard to Wilson (April 2002) (provided by Marrian Johnson).

> klipspringers, and, in a large glass corner case of its own, a huge mountain gorilla with its fangs bared, beating its chest." (Mitchell, 2005: 192).

Doug Smith, Professor of Biology at the University of Massachusetts (Amherst), who studied the Unionidae and Margaritiferidae, found Johnson's collegiality to be inspiring:

> "Dick was always very kind and generous to anyone who showed interest in his work and his contributions to the history of the study of Unionidae are unparalleled. During the 1980s, with attention being turned to the conservation of these animals, the collection of specimens for shell preservation alone became discouraged. Most states enacted the prohibition of collecting live animals. So during my fieldwork, I would start collecting only the shell remains of species as vouchers . . . . Not certain of the eventual disposition of my material, I would deposit them in the MCZ. Early in this practice, I would present Dick with a bag of shell remains with the comment, 'Dick, I brought you some 'skins'...' Incredulous, Dick would respond, "SKINS! You brought me SKINS!" I responded, 'They have data.' He would look into the bag muttering to himself, 'I shall soon enter this fine collection of 'SKINS' into the collection.' I will miss his disparaging wit and counsel." (D. G. Smith, in litt., 20 Aug. 2020).

After Clench retired in 1966, and Kenneth J. Boss (1935–2014), a former graduate student at the MCZ, became the new Curator of Malacology, Johnson and Boss became best friends, sharing lively conversations about a wide range of zoological, literary, and historical topics. They worked to build up the MCZ's Malacology library into one of the finest and easily accessible reference libraries on malacology – bolstered by Johnson's donations of rare books and reprints from obscure journals.

Johnson became well known to the graduate students that both Clench and Boss had over the decades from the 1950s through the 1980s, not only in sharing references from his personal library with them, but also as an amiable office mate who provided helpful discussions about the molluscan literature. Johnson also become well known to most of the curatorial staff and some of the graduate students elsewhere in the MCZ. For example, when Hamish Spencer (then a student of Richard Lewontin and now at the University of Otago, New Zealand) mentioned in the mid-1980s that his very first paper was just accepted by the *American Naturalist*, one of the most prestigious biological journals (now devoted primarily to theoretical and mathematical approaches to biology), Johnson was able to congratulate Spencer, remarking that he had recently read several papers in that same journal. Spencer was both surprised and impressed that Johnson was using this journal – but what Spencer did not realize is what Johnson left out with his characteristic elision – the articles Johnson had just read in the *American Naturalist* were Verrill's descriptions of new species of mollusks, published in the 1870s, a century earlier!

When Boss taught a Freshman Seminar on Darwin's *Voyage of the Beagle* for many years, Johnson also got to know some of those undergraduate students, one of whom remarked, two decades later, that Johnson and Boss were part "of a long line of inveterate humorists and pranksters to inhabit the recesses of the MCZ Mollusks Department." (Dean, 1999).

Johnson was known across the MCZ as a long active researcher; only the entomologist Edward O. Wilson (born 1929), who started graduate school at the MCZ in 1951 and is still writing books in 2020, has eclipsed Johnson's time at the MCZ (Figure 6). That said, Mitchell, in his "reimagined" biography of Robert Gilbert (1870–1942), the first African-American employee of the MCZ, erred when he stated that Johnson was among those who socialized with the herpetologist and MCZ Director Thomas Barbour: "One of the presiding judges of these last days of Barbour's *Eateria* [lunch club] was a man named Richard Johnson…" (Mitchell, 2005: 192). Johnson told me that as a high school student, while he saw Barbour (1884–1946) several times, the two never actually met let alone socialized, and it was not until the 1950s that Johnson began to know the MCZ curators and staff in the other areas of the museum.

In the early 1990s, Boss and Johnson decided that it would be appropriate to have an official portrait of Ernst Mayr (1904–2005), the ornithologist, evolutionary biologist, and MCZ Director from 1961 to 1970. They had admired the portrait of Professor Richard Evans Schultes (1915–2001), the ethnobotanist and explorer of South America, which was on display at the Botanical Museum. They learned that Robert Douglas Hunter painted Schultes in 1984, so they commissioned Hunter to do a similar portrait of Mayr, in time for the dedication of the Ernst Mayr Library at the MCZ in 1995 (Figure 5) (Boss, 1998: ii, vii).

Research on Unionoida

Clench, when he told the 14-year-old Johnson in 1939 that he was to work on the Unionidae, could never have imagined that Johnson's knowledge of that family would soon eclipse not only that of Clench but also that of nearly all the other students of that family. The Unionoida (the order containing the Unionidae and several smaller families) is by far the most speciose of freshwater bivalves, containing just over 850 living species, or over 70% of all freshwater bivalve species (Graf, 2013: 137).

From the 1900s through the 1960s, many researchers of the Unionidae had a parochial focus, only studying the fauna of one country or one river system. Even today, many unionid researchers are only knowledgeable about a geographical or taxonomic subset of this family. Johnson soon realized that in order to curate the MCZ's worldwide collection, and to understand the relationships among the species and genera, he had to expand his knowledge to the entire family. Although Johnson's own publications were primarily on the North American unionid fauna, which itself has more species than any other continent, he was

able to identify species from elsewhere in the world and discuss genera from around the world. Probably only Fritz Haas (1886–1969), long-time curator at the Senckenberg Museum (Frankfurt) before escaping from the Nazis to the Field Museum (Chicago), had a comparable encyclopedic knowledge of this family.

While some of Johnson's papers on this family were short notes on individual species or closely related species, including describing six new species (*infra*), he also authored four monographs that remain key references for unionid researchers, decades later. The first was his paper on the Southern Atlantic Slope unionid fauna (1970c), which synthesized numerous museum records and widely scattered literature citations to this fauna, from St. Mary's River in northern Florida to the Potomac River in Maryland. Johnson was able to reconcile and synonymize numerous species that had been described multiple times by different authors, leading to the recognition of 15 genera and subgenera comprising 40 species and subspecies.

The second key paper was on the Unionidae of peninsular Florida, *i.e.*, south of St. Mary's River, and excluding the western Panhandle region (1972c). This fauna is far more limited, comprising only 8 genera and 12 species, with 10 of those species also being found outside of Florida. This fauna reflects the oceanic submergence of peninsular Florida during Pliocene and Pleistocene times, followed by the subsequent repopulation from the north.

His third key paper was on *Plagiola*, a quite speciose genus (with 5 subgenera and 17 species) found mostly in the Tennessee River system and adjacent inland waters (1978). *Plagiola* (= *Epioblasma*) is one of the few unionid genera whose shells have marked sexual dimorphism, which resulted in earlier authors describing the males and females as separate species, and Johnson did much to clear up the confusion in the literature. This was essentially a paleontological paper – thanks to the numerous dams built on the Tennessee River by the Tennessee Valley Authority (TVA) in the 1930s, many of the species are long extinct.

His fourth key paper was on the biogeography and systematics of the unionids (10 genera and 14 species) north of the Pleistocene glaciation, *i.e.*, species that recolonized the area around the Great Lakes and adjacent regions after the glaciers receded at the end of the Ice Age (1980).

Taken together, these four monographs could have qualified Johnson for tenure at almost any museum or university at that time. The Freshwater Mollusk Conservation Society awarded Johnson with the Lifetime Achievement Award in 2001 for his "contributions to freshwater malacology through taxonomy, biogeography, bibliography, and biography." In the early 1990s, when I was working at the Smithsonian's National Museum of Natural History, I twice observed visiting researchers carefully examining type specimens of Unionidae – both times, the researcher was holding the Southern Atlantic Slope paper (1970c) in one hand, and a shell in the other hand. Afterwards, I remarked to Johnson that this is what the "re" in "research" meant!

Johnson's monographs reflected his extensive collecting efforts, including several trips made with his family, sometimes accompanied by Samuel Fuller. At the 1962 AMU meeting (St. Petersburg, Florida), where Johnson gave a talk on "Collecting freshwater shells in Florida" (1962: 7), Margaret Teskey, the meeting recorder, quoted Johnson, somewhat tongue-in-cheek:

> "Mr. Johnson together with his family had collected Unionidae *en route* to the meeting. He mentioned briefly some of the problems which beset shell collectors, especially collectors of land and freshwater species. Not the least of these is the curiosity of the uninformed onlooker. There are a number of answers to 'What are you doing? Why do you want those clams – or those snails?' 'For bait,' is easily understood and usually serves to satisfy. 'We sell them,' may also serve but may lead to complications as the inquirer seeks to ascertain a market for his own future efforts. To say 'We are collecting *Elliptio complanatus*' will on occasion buy respectful silence. Best of all, said Mr. Johnson, was his young daughter's inspired rejoinder to a questioner: 'I'm looking for their souls!'"
>
> Finally, said he, after one has collected *en route* and cooked out the daily take in motel rooms, it is well to select a wholly new set of motels on the return trip (1962: 8).

Johnson's most frequently cited paper is an archaeological paper published in *Science*, for which he contributed the identifications of the freshwater bivalves (1991b). Anna Roosevelt, then at the Field Museum (Chicago), and several colleagues in Brazil discovered a giant shell midden in the Amazon Basin which had the oldest known pottery ever found in the Western Hemisphere, from the 8th century B.C. They had to identify the shells in this shell midden and, as Johnson was familiar with the freshwater bivalves of Brazil, he was able to identify three species of Unionidae among the shells. Johnson later remarked (1996a: 83) that, since his coauthors were back in Brazil at the time the paper was published, he got the calls from the reporters (radio stations and newspapers) about this significant discovery, but he was, alas, unable to tell the reporters much beyond the identity of the shells involved.

History of Malacology

Although Johnson's expertise was the Unionidae, he is equally well known to malacologists who study other groups of mollusks, thanks to his extensive biographical and bibliographical research on a wide range of molluscan researchers and collectors over the past several centuries. Those papers similarly remain valuable references, as Johnson did much to clear up confusion over publication dates, particularly of works that were published in multiple parts over a period of several years or even decades. In the 1800s and even into the early 1900s, it was common for books and encyclopedic works to be published in

sections, with each section issued to subscribers at the time it was printed. The subscriber would then have to bind the entire work into volumes upon completion of the publication. All too often, the publisher failed to provide accurate information on the publication date of each part, or that information would only be on the paper covers to the individual sections – covers that typically were discarded when the volumes were bound. Johnson, aided by his remarkably broad personal library, was able to determine the accurate publication dates for many of these problematic works.

Although Johnson was comprehensive in preparing his manuscripts, sometimes "even Homer nods," and he missed a species or an article. Fortunately, he was saved in writing his lengthy manuscript on Verrill and Bush (1989) – shortly before it was to be published, I asked him about *Octopus giganteus*, which Verrill had described from a giant "blob" found on a beach in Florida, as I had seen citations to this enigmatic species. Johnson, startled, realized that he had omitted this species, the largest-sized *Octopus* species ever described, and he was able to add it to his manuscript at the last minute (1989: 17, 39). As the "cryptozoologists" were interested in this species, which they speculated would have been an impossible 200 feet in size, I made the mistake of suggesting that Johnson send his 1989 paper to those cryptozoologists, who used it as a springboard to continue publishing on this supposed *Octopus*. Several years later, other zoologists found fragments of the original specimen from Florida, and determined that this was actually whale blubber (Pierce et al., 1995). Johnson was able to publish an update (1998b; see also Pierce et al., 2004), ending the fevered speculations of cryptozoologists.

Biographical and Historical Publications

In reviewing the breadth of the following lists, it is safe to say that nobody else has published so widely and deeply on the history of malacology. Johnson's biographical and bibliographical research can be divided into six categories. The first category consists of his papers on others who studied the Unionidae – research that was necessary for Johnson to do his own research on the systematics of that family and to curate the MCZ's growing collections:

Call, R. Ellsworth (1975c);
Heude, Pierre Marie (1973d);
Frierson, Lorraine Screven (1972a);
Fuller, Samuel L.H. (2002i; 2002k);
Grier, Norman MacDowell (1977b);
Gray, Arthur Fairfield (2002c);
Lamarck, J.B.P.A. (1952, 1953, 1969f);
Lea, Isaac (1974b);
Marsh, William A. (1975d);
Marshall, William B. (1974c);
Ortmann, Arnold Edward (1977c);
Rafinesque, Constantine Samuel (1973a);
Simpson, Charles Torrey (1975f);
Spengler, Lorentz (2003a);
Utterback, William Irvin (1969c);
Wheatley, Charles M. (1959b); and
Wright, Berlin H. and Samuel H. (1967a).

Johnson's fellow researchers on the Unionidae have much appreciated these papers – even if Johnson had published nothing else on the family, his biographical and bibliographical articles on these researchers have greatly facilitated the research of others on this family. That said, David Stansbery, the long-time curator at the Ohio State University Museum of Zoology, upon seeing Johnson's paper on Ortmann – who had also published on the Ohio River fauna – exclaimed, "Ortmann was my project!" As far as is known, this is the only time that Johnson "scooped" another researcher, although in retrospect it is unlikely that Stansbery ever would have completed his own project.

The second category consists of his papers on other malacologists and collectors, particularly from New England. The two longest such papers, which each took several years to research, were on (1) Augustus A. Gould (1805–1866) of the Boston Society of Natural History (1964, along with two meeting abstracts, 1956a and 1960), and (2) Addison E. Verrill (1839–1926) and Katharine J. Bush (1855–1937) of Yale University's Peabody Museum of Natural History (1989). Yet other papers included treatments of the following individuals:

Adams, Charles Baker (1972b, 2006b);
Bequaert, Joseph Charles (2006g);
Blaney, Dwight (2009);
Boss, Kenneth Jay (2015);
Brooks, Stanley Truman (1981a);
Clench, William James (2003b, 2006h);
Couthouy, Joseph Pitty (1946a, 1954a, 2006e);
Merrill, Arthur Stewart (2010a, 2010b);
Mighels, Jesse Wedgwood (1949b, 1954b, 2002f);
Newcomb, Wesley (1996b, 2002g, 2006b);
Pease, William Harper (1994b, 1996b, 2002g);
Temple (1959a, 2006b);
Procter, William (2009);
Smith, Sanderson (1989);
Storer, David Humphreys (2006i);
Taylor, Dwight Willard (2008);
Turner, Ruth Dixon (2003b, 2006h);
Verrill, Alpheus Hyatt (1989); and
Wetherby, Alfred Gallatin (2002a).

One issue that should be noted with respect to several of Johnson's earlier publications is the treatment of an author's original specimens. Today, Article 73 of the *International Code of Zoological Nomenclature* (ICZN, 1999) provides that, when describing a new species based on more than one specimen, the author can either designate one specimen as the "holotype" and the remaining specimens will become "paratypes," or the author can explicitly state that the type specimens are all "syntypes." If an earlier author had not designated one specimen as the holotype, then under the current *Code*, all of the author's specimens are "syntypes" and it is up to subsequent researchers to designate one of the syntypes as

the "lectotype," with the remaining becoming "paralectotypes." However, from Linnaeus in the 1750s through the early 1900s, authors often did not indicate which specimen was the holotype, or even whether a new species was based on more than one specimen. Hence, many researchers in the mid- to late-1900s often stated that the "figured specimen" was the holotype, which Johnson did, and later researchers would then interpret those as "lectotype" designations. Nobody could have predicted that the *Code* would be amended in later years to negate many of these designations or selections, with the result being that the original specimens were now back to being syntypes (ICZN, 2003). Although ICZN Article 74.6 allows for the "fixation" of a lectotype by inference of the holotype, that only applies "where it has been accepted that a nominal species-group taxon was based on a single specimen," which is not always the case. Johnson later recognized this problem with respect to some of his "neotypes" of Mighels species (2002f), and other authors have discussed this with respect to Johnson's characterization of the type material of Gould, Verrill, and Bush (Souza and Pimenta, 2019: 427–429; Yeung et al., 2017: 3–4).

The third category consists of his papers that set forth the publication history and dates for several multipart malacological treatises:

Chenu, *Illustrations Conchyliologiques* [1843–1853] (1963).
Costa, O.G. and A. Costa, molluscan portions (including the brachiopods) of the *Fauna del Regno di Napoli* [1829–1886] (1984c).
Hombron and Jacquinot, molluscan sections of the *Voyage au pôle sud et dans l'Océanie sur les corvettes l'Astrolabe et l'Zélée exécuté par ordre du Roi pendant les années 1837–1838–1839–1840 sous le commandement de M. Dumont d'Urville* ... [1847–1854] (2006d).
Martini and Chemnitz (Küster's edition) *Systematisches Conchylien–Cabinet* [1837–1920] (1968a).
Pfeiffer, *Novitates Conchologicae*, Series I, Land Mollusca [1854–1879], and Dunker, *Novitates Conchologicae*, Series II, Marine Mollusca [1862–1882] (1969e).
Rossmässler, *Iconographie der Land- und Susswasser-Mollusken, Europa's*, continued by W. Kobelt [1835–1920] (1969b).
Semper, *Reisen im Archipel der Philippinen, Wissenschaftliche Resultate* [1867–1916] (1969a).

The fourth category consists of museum type catalogs, *i.e.*, lists of original specimens that formed the basis for an author's description of a new species. With one exception, these are of type specimens in the Unionoidea and Hyrioidea ("Mutelacea"):

Academy of Natural Sciences of Philadelphia (1973e; 1980b);
British Museum (Natural History) (1971a);
MCZ (1956b);
MCZ – Corbiculidae and Sphaeriidae (1959a); and
Museum of Zoology, University of Michigan (1979).

The fifth category consists of narrative histories of the mollusk collections and research at several natural history museums:

Boston Society of Natural History (2002d, 2004);
Carnegie Museum, Pittsburgh, Pennsylvania (1977d);
Museum of Comparative Zoology (2006h);
Lyceum of Natural History of New York (2006b); and
Portland Society of Natural History, Maine (1997c).

Johnson's reports on the Boston Society of Natural History (BSNH), which drew upon his recollections of having studied there in the early 1940s, are particularly valuable in having documented the history of that important, yet largely forgotten institution. Indeed, modern science historians have criticized the Boston Museum of Science (the successor to the BSNH) for ignoring its own history and for not presenting scientific discoveries in their historical context (Cain, 2017: 385). In contrast, the preservation of the historic exhibits at the MCZ and the adjacent Botanical Museum (with the Blaschkas' Glass Flowers) "has allowed visitors to contemplate older modes of scientific thought and knowledge production in Boston" (Cain, 2017: 387); since Johnson's MCZ office opened directly off the historic two-story "Great Mammal Hall," he was part of that very history.

Last but not least, the sixth category consists of his shorter notes on individual publications and several researchers, sometimes based on unique books in his possession, and sometimes with humorous or ironic observations:

Aldrich, Truman Hemenway (2002a);
Anthony, John Gould (2006b);
Binney, William Greene (2006b);
Bland, Thomas (2006b);
Born, Ignaz Edler (1984d);
Buonanni, Philippo [Filippo Bonanni] (1984e);
Doherty, William (2002a);
du Pont, John E. (2006c);
Green, Jacob (2002h);
Holmes, Oliver Wendell (1998c, 1999g);
Jay, John Clarkson (1998d, 1999f, 2006b);
Charles-Alexandre (2002b);
Perry, *Conchology* [1811] (1970a);
Poe, Edgar Allan (1974d);
Redfield, John Howard (2006b);
Reeve and Sowerby, *Conchologia Iconica* [1843–1878] (1970b);
Say, Thomas, *Conchology* [1817] (1975g);
Thevet, André, *Cochlea sarmatica* [1575] (2002e);
Warren, Gretchen Osgood (1999d);
Warren, John, *The Conchologist* [1834] (1999e); and
Wyatt, Thomas (1974d).

One common thread across many of these latter papers was Johnson's ability to trace unexpected historical and literary connections to various malacological topics. This is reflected in his apt statement, during his COV talk on

molluscan rare books, in referring to a particularly obscure fact relating to the philosopher Erasmus (1466–1536), that "It is often difficult to bring this interesting and important fact into general conversation" (1996a: 84; Reed, 1998: 108). This approach is reflected in some of these historical papers whose seemingly dry titles hide interesting nuggets. Who knew that Edgar Allan Poe put his name on a plagiarized student text book, *The Conchologist's First Book*, which went through three editions? (1974d). That Frances Trollope, one of the first Englishwomen to write a book about travels in the United States, visited Cincinnati (Ohio) in 1827, and specifically praised Joseph Dorfeuille, the curator of the natural history museum in Cincinnati who collected land snails? (2002a: 113–114, 122). That Oliver Wendell Holmes, the physician/poet and father of the Supreme Court Justice, wrote a poem, *The Chambered Nautilus*, based on both *Argonauta* and *Nautilus*, but one which perhaps borrowed too much from the literary efforts of others? (1998c, 1999g). That Joseph Couthouy, the subject of Johnson's first historical paper (1946), was extensively tattooed by the South Pacific natives in the late 1830s while serving as the "Conchologist" on the U.S. Exploring Expedition? (2006e). That Ignaz von Born, author of an important conchological treatise in 1778, also authored a sarcastic illustrated "classification" of monks? (1984d). And so on – numerous other nuggets reflect both Johnson's wide reading and his ability to find something interesting in seemingly any topic.

New Species and an Eponym

Johnson described six new species of freshwater mussels in the superfamily Unionoidea (Mollusca: Bivalvia). These species and their names are of unexpectedly broader interest.

First, Johnson described three species after three women in his life. His very first species, *Hyridella fannyae*, which he described in 1948 while a sophomore (second-year student) in Harvard College, was named after Fanny Day Farwell (1927–2007), his then-girlfriend and a senior at Vassar College (New York). His second species, *Anodonta peggyae*, was named in 1965 after Peggy Johnson, his first wife. Finally, *Margaritifera marrianae* was named in 1983 after Marrian Johnson, shortly after he married her that same year.

In a coffee-table book on the treasures of the MCZ, Pick (2004: 83) noted that Johnson had "a sense of humor" in stating that *H. fannyae* "was 'appropriately named' for his sweetheart at the time," as it was a particularly "shapely mussel." Dance (2009: 574) included this species in a humorous commentary on unusual molluscan names.

When *peggyae* and *marrianae* were both included in the book, *Freshwater Mussels of Alabama* (Williams et al. 2008), Johnson remarked to his colleagues that this was "the first time that both of my wives were under the same cover," albeit separated by 650 pages.

Second, Johnson described three other species, each with a "portmanteau" species name that honored two or three other malacologists. While zoologists sometimes name species after each other, it is unusual for one species to be named after two or more unrelated persons, yet Johnson did this three times. *Elliptio steinstansana* (= *Parvaspina steinstansana*), described in 1983 from North Carolina, honors the two malacological curators at the Ohio State University Museum of Zoology, Carol B. Stein (1937–2010) and David H. Stansbery (1926–2017). *Lampsilis fullerkati* (= *L. radiata*), described in 1984 from North Carolina, recognizes both Samuel L. H. Fuller (1942–2001) and Pieter W. Kat (born 1954), both of whom then worked extensively on the Unionidae. *Potamilus metnecktayi*, described in 1998 from Texas, honored not two but three malacologists, Artie L. Metcalf (1929–2016), Raymond W. Neck (1946–2017), and Dwight W. Taylor (1932–2006). It is not known where Johnson got the idea of naming a species after two or three unrelated persons, but other malacologists have copied this idea, as another species of *Potamilus* from Texas, *P. streckersoni* Smith et al., 2019, was recently named after both John K. Strecker (1875–1933) and Lorraine S. Frierson (1861–1936).

Hyridella fannyae, now placed in *Haasodonta*, is intrinsically interesting as a potential exception to a key "law" of biogeography, the so-called "Wallace's Line," the biogeographic barrier between the non-marine fauna of Southeast Asia (the Asian tectonic plate) and that of Australia, New Guinea, and the eastern islands of Indonesia (the Australian tectonic plate). Relatively few land and freshwater animal and plant species are found on both sides of Wallace's Line, named after Alfred Russel Wallace (1823–1913). Don McMichael, a recent graduate student at the MCZ, described *Haasodonta* as a new genus of the Unionidae from "Dutch New Guinea," now Irian Jaya, the easternmost province of Indonesia (McMichael, 1956). McMichael and Hiscock (1958: 483–485) noted that *Haasodonta* was the only Australasian member of the Unionidae, as all the other taxa of freshwater mussels from eastern Indonesia, New Guinea, and Australia are instead referable to the family Hyriidae. Graf and Cummings (2009: 233) noted that "we find it plausible . . . that a single lineage of Unionidae [*Haasodonta*] may have breached Wallace's Line to invade Australasia from the Sunda Islands." Similarly, Walker (2016: 19) noted that nearly all the freshwater mussels of New Guinea are in the Hyriidae, but "*Haasodonta* probably is not a member of the Hyriidae, but one of the Unionidae," which would make this genus "the only freshwater mussels known to have crossed Wallace's Line," either by fish or human transport. Due to heavy industry and development projects in eastern Irian Jaya, *Haasodonta* may now be extinct, so that living specimens probably cannot be obtained (Walker, 2016: 20). In a recent molecular genetic analysis of the Unionoida, *Haasodonta* remains "*incertae sedis*" due to lack of living specimens for molecular analysis (Pfeiffer et al., 2019: 124). Thus, further research is needed to determine the actual placement of this enigmatic taxon, the only Asian

genus of the Unionidae to be found east of Wallace's Line.

Finally, one species was named after Johnson – Arthur H. Clarke, who did his thesis at the MCZ on deep-water marine mollusks before switching to the freshwater Unionidae, described the deep-water marine bivalve *Malletia johnsoni* in 1961. When the MCZ had a public exhibit in 1989 of species named by and for MCZ researchers, one display included not only the three species that Johnson named after his then-girlfriend and his wives, but also *Malletia johnsoni*. At the opening night exhibit reception, a female friend exclaimed to Johnson, upon seeing this species (which is 4 to 6 mm long, or less than one-quarter of an inch), "But Richard, it's so *small*!" and his ineffective rejoinder was, "That's not the point!"

New Species:

Acronyms: MCZ: Museum of Comparative Zoology; NMC: National Museum of Canada; OSUM: Ohio State University Museum of Biological Diversity; UMMZ: University of Michigan Museum of Zoology; USNM: National Museum of Natural History, Smithsonian Institution; UTEP: University of Texas at El Paso, Biodiversity Collections.

fannyae, *Hyridella* – Johnson, 1948, The Nautilus, 62(2): 47–48, pl. 3, fig. 1. Type locality: Merauke, Marco River, Dutch New Guinea [Maro River, Irian Jaya, Indonesia]. Holotype, MCZ 160663. A second specimen of this species was illustrated by Pick (2004: 83). Type species by monotypy of *Haasodonta* McMichael, 1956: 47–48, pl. 2, figs. 3–5. *Haasodonta fannyae* (Johnson, 1948), *fide* McMichael and Hiscock (1958: 483–485).

fullerkati, *Lampsilis* (*Lampsilis*) – Johnson, 1984, Occasional Papers on Mollusks, 4(63): 307–310, pl. 42, figs. 1–3. Type locality: Lake Waccamaw, Columbus County, North Carolina, U.S.A. Holotype MCZ 294576; paratypes MCZ 294577 and MCZ 294578. A junior synonym of *Lampsilis radiata* (Gmelin, 1791), *fide* McCartney et al. (2016) and Williams et al. (2017: 40).

marrianae, *Margaritifera* – Johnson, 1983, Occasional Papers on Mollusks, 4(62): 299–303, pl. 41, figs. 2–3. Type locality: Hunters Creek, 8 miles southwest of Evergreen, Conecuh County, Alabama, U.S.A. Holotype, MCZ 28491; paratypes MCZ 62595 and MCZ 148819. Smith (2001: 40, 42) transferred this species to the genus *Pseudunio*; Lopes-Lima et al. (2018: 112) determined that this species belonged in *Margaritifera sensu strictu*, which was also used by Williams et al. (2008: 98–100; 2011: 10; 2017: 36).

metnecktayi, *Potamilus* – Johnson, 1998, Occasional Papers on Mollusks, 5(76): 429–433, pl. 22, figs. 1–2. Type locality: Rio Salado, 45 miles south of Nuevo Laredo, Tamaulipas, Mexico. Holotype, UMMZ 255018; paratypes UMMZ 255019, UMMZ 66993; UTEP 2519. *Potamilus metnecktayi* Johnson, 1998, *fide* Karatayev et al. (2012), Bosman (2015: 15), and Smith et al. (2020: 517).

peggyae, *Anodonta* – Johnson, 1965, Breviora, 213: 1–7, pls. 1–2. Type locality: southeast shore of Lake Talquin, Ochlockonee River, Leon County, Florida, U.S.A. Holotype, MCZ 251040; paratypes MCZ 191840 and MCZ 251041. *Utterbackia peggyae* (Johnson, 1965), *fide* Bogan and Hoeh (1995) and Williams et al. (2008: 753–755; 2011: 54; 2017: 44).

steinstansana, *Elliptio* (*Canthyria*) – Johnson and Clarke, 1983, Occasional Papers on Mollusks, 4(61): 291-294, pl. 40, figs. 4–5. Type locality: Tar River, 1.5 miles north of Tarboro, Edgecombe County, North Carolina, U.S.A. Holotype, MCZ 282677; paratypes MCZ 267438, MCZ 282676, MCZ 282678, MCZ 282784, MCZ 293570; USNM 758667. The authors listed MCZ 282678 twice; the second record is in error. The authors also listed a lot from the Ohio State Museum ("Old Sparta," two paratypes collected by Carol B. Stein in 1964), which may be OSUM 17578 (but that lot has three specimens, collected by Stein in 1963; I. Roznere, *in litt.*, 7 Aug. 2020); perhaps the 1983 description of this lot was in error. *Parvaspina steinstansana* (Johnson and Clarke, 1983), *fide* Perkins et al. (2017: 755).

Eponym:

johnsoni, *Malletia* – Clarke, 1961, Bulletin of the Museum of Comparative Zoology, 125(12): 370–371, pl. 2, fig. 6. Type locality: *R/V Vema* Station 22 (1,675 fathoms, Angola Basin, about 175 miles west of Banana, Congo). Holotype, MCZ 224961; six paratypes NMC 4737 and NMC 20026. *Malletia johnsoni* Clarke, 1961, *fide* Sanders and Allen (1985: 205–211), although La Perna (2003: 28) suggested that this species "appears somewhat intermediate between *Neilo* and *Pseudomalletia*."

Publications

Johnson amassed a remarkably extensive publication record, particularly given that this was entirely volunteer work. From 1941 to his last malacological paper in 2015, a span of 74 years, he published a total of 135 papers on mollusks (including several abstracts and book reviews), amounting to 2,567 pages. Johnson came within two years of eclipsing the publication span of Pilsbry, whose first paper was published in 1882 (at the age of 20) and whose last paper was published 76 years later, in 1958, shortly after Pilsbry died.

Johnson's publications can be categorized as (1) 723 pages on the systematics and biogeography of the Unionidae; (2) 724 pages of biographies and bibliographies on those who specifically studied and collected the Unionidae; (3) 1,080 pages of biographies and bibliographies of other malacologists and collectors; (4) 26 pages on freshwater gastropods; and (5) 14 pages of book reviews.

Another way of analyzing this output is that 1,234 pages of his research were published in malacological journals; 648 pages were published in the *Bulletin of the Museum of Comparative Zoology*; and the remainder were published in a range of other scientific journals. Johnson contributed significantly to three malacological journals. The first was *Occasional Papers on Mollusks* (OPM), which Clench founded in 1945, at a time when there was only one other general malacological journal in the United States, *The Nautilus*, which then did not have high-quality illustrations or artwork. OPM continued through 2002, with a total of 2,572 pages.[3] The second was the *Special Occasional Publications* of the MCZ Mollusk Department, a more inexpensively printed journal that ran from 1973 to 1992. After OPM ended, Johnson had a backlog of papers, so he published a one-time-only journal, *Sporadic Papers on Mollusks*, which had eight historical articles (in three issues), running to 173 pages (2006b – 2006i). This latter journal was sent to the same subscription list as for OPM, thereby ensuring its distribution.

Johnson remarked, somewhat facetiously, that "Old conchologists don't retire: they just keep moving shells from one box to another. That's called 'trying to study evolution.'" (1991a: 94). Although he described his last new species in 1998, his remaining publications from 1991 onwards were primarily historical and biographical. In the 1990s, Johnson started researching a companion paper to his 1970 "Southern Atlantic Slope" monograph, which would have covered the unionid fauna from the Potomac River (Maryland) northwards to Nova Scotia (Canada), and he began to assemble the literature records and museum locality records. However, he eventually realized that the proliferation of the "grey literature" (government agency reports and contract surveys, both hard to find), and the increasing use of molecular techniques to differentiate species, would make it impossible to complete his research. He also contemplated, but did not start, a comprehensive history, tentatively titled *Conchology: The American Experience*, which he called an "old age project" (2006a: 78), as a counterpart to Dance's somewhat Eurocentric history of conchology (Dance, 1986). That said, a comprehensive history of the study and collecting of mollusks in the New World remains to be written.

Bibliography

Note: The references are in chronological order regardless of authorship. The publication dates for articles in *The Nautilus* are from Coan and Harasewych (1993); the dates for articles and abstracts of the American Malacological Union's / Society's publications are from Coan and Kabat (2007).

Johnson, R.I. 1941 [5 May]. *Viviparus contectoides* Binney in Massachusetts. The Nautilus 54(4): 141.

Johnson, R.I. 1945 [20 June]. *Radix auricularia* (Linn.) in Vermont. The Nautilus 58(4): 144–145.

Johnson, R.I. 1946a [14 February]. Joseph Pitty Couthouy – a bibliography and catalogue of his species. Occasional Papers on Mollusks 1(5): 33–40 (including pl. 8) [see 1954a and 2006e for updates].

Johnson, R.I. 1946b [2 August]. *Anodonta implicata* Say. Occasional Papers on Mollusks 1(9): 109–116 (including pl. 16).

Johnson, R.I. 1947a [April]. Unionidae of New England [abstract]. American Malacological Union, News Bulletin and Annual Report for 1946: 3.

Johnson, R.I. 1947b [22 September]. *Lampsilis cariosa* Say and *Lampsilis ochracea* Say. Occasional Papers on Mollusks 1(12): 145–156 (including pls. 19–21).

Johnson, R.I. 1948a [22 July]. The authorship of *Elliptio complanatus*. The Nautilus 62(1): 36.

Johnson, R.I. 1948b [8 December]. A new naiad from Dutch New Guinea. The Nautilus 62(2): 47–48, pl. 3, fig. 1.

Johnson, R.I. 1948c [8 December]. Lectotypes for two species of Asiatic Unionidae in the genus *Pseudodon*. The Nautilus 62(2): 48–51, pl. 3, figs. 2–3 [see 1950a for update].

Johnson, R.I. 1949a [18 March]. The lost type of *Obovaria depygis* (Conrad). The Nautilus 62(3): 102.

Johnson, R.I. 1949b [30 March]. Jesse Wedgwood Mighels, with a bibliography and a catalogue of his species. Occasional Papers on Mollusks 1(14): 213–231 (including pls. 26–27) [see 1954b and 2002f for update].

Johnson, R.I. 1950a [4 April]. On the selection of lectotypes. The Nautilus 63(4): 125 [update to 1948c].

Johnson, R.I. 1950b [December]. *The shell collector's handbook*, by A. Hyatt Verrill [book review]. Bulletin of the Massachusetts Audubon Society 34(8–9): 354.

Johnson, R.I. 1951a [15 February]. A clarification of some Central American Unionidae described by R. A. Philippi. The Nautilus 64(3): 77–83, pl. 5, figs. 1–2.

Johnson, R.I. 1951b [27 August]. A rectification of some Central American Unionidae. The Nautilus 65(1): 32–33 [update to 1951a].

Johnson, R.I. 1951c [27 August]. *Shell collector's handbook*, by A. Hyatt Verrill [book review]. The Nautilus 65(1): 36.

Johnson, R.I. 1951d [28 September]. Dezallier D'Argenville 1742: *L'histoire naturelle eclaircie dans deux de ses parties principales: La lithologie et la conchyliologie* [book review]. Johnsonia 2(30): 288.

Johnson, R.I. 1952 [17 November]. A study of Lamarck's types of Unionidae and Mutelidae [part 1]. The Nautilus 66(2): 63–67.

Johnson, R.I. 1953 [2 February]. A study of Lamarck's types of Unionidae and Mutelidae [part 2]. The Nautilus 66(3): 90–95.

Johnson, R.I. 1954a [14 August]. Supplement to Joseph Pitty Couthouy. Occasional Papers on Mollusks 1(18): 441–442 [update to 1946a].

Johnson, R.I. 1954b [14 August]. Supplement to Jesse Wedgwood Mighels. Occasional Papers on Mollusks 1(18): 446–447, pl. 58, fig. 1 [update to 1949b].

Johnson, R.I. 1955 [January]. A few old shell books [abstract]. American Malacological Union, Annual Report 1954: 3.

Johnson, R.I. 1956a ["1955"] [April]. Augustus Addison Gould [abstract]. American Malacological Union, Annual Reports for 1955: 12–13.

[3] OPM should not be confused with the *Occasional Molluscan Papers*, a journal founded in Singapore in 2008, and devoted to the systematics of the molluscan fauna of Southeast Asia.

Johnson, R.I. 1956b [September]. The types of Naiades (Mollusca: Unionidae) in the Museum of Comparative Zoology. Bulletin of the Museum of Comparative Zoology 115(4): 101–142, pls. 1–2.

Johnson, R.I. 1958 [January]. A visit to Thomas Say's New Harmony [abstract]. American Malacological Union, Annual Reports for 1957: 7–8.

Johnson, R.I. 1959a [May]. The types of Corbiculidae and Sphaeriidae (Mollusca: Pelecypoda) in the Museum of Comparative Zoology, and a bio-bibliographic sketch of Temple Prime, an early specialist of the group. Bulletin of the Museum of Comparative Zoology 120(4): 431–479, pls. 1–8.

Johnson, R.I. 1959b [30 October]. The Charles M. Wheatley collections. The Nautilus 73(2): 72–74.

Johnson, R.I. 1960 [January]. Unearthing Gould's types [abstract]. American Malacological Union, Annual Reports for 1959: 12–13.

Johnson, R.I. 1961 [April]. Richard Irwin Johnson. Pages 102–103, in (H. D. Lewis, ed.), Harvard College Class of 1951 Decennial Report. Cambridge: Harvard Univ., xxxii + 250 pp.

Johnson, R.I. 1962 [21 December]. Collecting freshwater shells in Florida [abstract]. American Malacological Union, Annual Reports for 1962: 7–8.

Johnson, R.I. 1963 [January]. The arrangement and contents of the genera described in J.C. Chenu's *Illustrations Conchyliologiques* (1843–53). Journal of the Society for the Bibliography of Natural History 4(2): 92–95.

Johnson, R.I. 1964 [28 July]. The Recent Mollusca of Augustus Addison Gould: illustrations of the types described by Gould with a bibliography and catalog of his species. United States National Museum Bulletin 239: 1–182, pls. 1–45.

Johnson, R.I. 1965 [11 January]. A hitherto overlooked *Anodonta* (Mollusca: Unionidae) from the Gulf drainage of Florida. Breviora 213: 1–7 (including pls. 1–2).

Johnson, R.I. 1966 [April]. Richard Irwin Johnson. Pages 97–98, in (H. D. Lewis, ed.), Harvard College Class of 1951 Fifteenth Anniversary Report. Cambridge: Harvard Univ., xxix + 234 pp.

Johnson, R.I. 1967a [8 February]. Illustrations of all the mollusks described by Berlin Hart and Samuel Hart Wright. Occasional Papers on Mollusks 3(35): 1–35 (including pls. 1–13).

Johnson, R.I. 1967b [24 April]. *Carunculina pulla* (Conrad), an overlooked Atlantic drainage unionid. The Nautilus 80(4): 127–131.

Johnson, R.I. 1967c [29 June]. Additions to the unionid fauna of the Gulf drainage of Alabama, Georgia and Florida (Mollusca: Bivalvia). Breviora 270: 1–21 (including pls. 1–3).

Johnson, R.I. 1968a [January]. Martini and Chemnitz (Kuester's edition) *Systematisches Conchylien-Cabinet*, 1837–1920, a complete collation. Journal of the Society for the Bibliography of Natural History 4(7): 363–367.

Johnson, R.I. 1968b [24 July]. *Elliptio nigella*, overlooked unionid from Apalachicola River system. The Nautilus 82(1): 20, 22–24 (including pl. 1).

Johnson, R.I. 1969a [April]. Semper's *Reisen im Archipel der Philippenen* [sic], *Wissens[c]haftliche Resultate*, 1867–1916; a complete collation. Journal of the Society for the Bibliography of Natural History 5(2): 144–147 [note: the text of the article has the book title correctly spelled, but the article title does not].

Johnson, R.I. 1969b [April]. Rossmassler's *Iconographie der Land- und Susswasser-Mollusken, Europa's*, continued by W. Kobelt, 1835–1920; a complete collation. Journal of the Society for the Bibliography of Natural History 5(2): 148–151, pl. 2.

Johnson, R.I. 1969c [18 April]. The Unionacea of William Irvin Utterback. The Nautilus 82(4): 132–135.

Johnson, R.I. 1969d [28 July]. Further additions to the unionid fauna of the Gulf drainage of Alabama, Georgia and Florida. The Nautilus 83(1): 34–35.

Johnson, R.I. 1969e [October]. Pfeiffer's *Novitates Conchologicae*, Series I, Land Mollusca, 1854–1879, and Dunker's *Novitates Conchologicae*, Series II, Marine Mollusca, 1862–1882; a complete collation. Journal of the Society for the Bibliography of Natural History 5(3): 236–239.

Johnson, R.I. 1969f [31 October]. Illustrations of Lamarck's types of North American Unionidae mostly in the Paris Museum. The Nautilus 83(2): 52–61 (including pls. 1–5).

Johnson, R.I. 1970a [April]. Perry's *Conchology* (1811) – more than one edition. Journal of the Society for the Bibliography of Natural History 5(4): 287.

Johnson, R.I. 1970b [April]. Reeve, L. A., and G. B. Sowerby, *Conchologia Iconica* (1843–78): the original pattern set. Journal of the Society for the Bibliography of Natural History 5(4): 288.

Johnson, R.I. 1970c [27 November]. The systematics and zoogeography of the Unionidae (Mollusca: Bivalvia) of the Southern Atlantic Slope Region. Bulletin of the Museum of Comparative Zoology 140(6): 263–450 (including pls. 1–22).

Johnson, R.I. 1971a [20 January]. The types and figured specimens of Unionacea (Mollusca: Bivalvia) in the British Museum (Natural History). Bulletin of the British Museum (Natural History), Zoology 20(3): 73–108, pls. 1–2.

Johnson, R.I. 1971b [April]. Richard Irwin Johnson. Page 101, in (H. D. Lewis, ed.), Harvard College Class of 1951 Twentieth Anniversary Report. Cambridge: Harvard Univ., xlv + 248 pp.

Johnson, R.I. 1972a [2 June]. Illustrations of all of the mollusks described by Lorraine Screven Frierson. Occasional Papers on Mollusks 3(41): 137–173 (including pls. 22–32).

Johnson, R.I. and K.J. Boss, 1972b [2 June]. The fresh-water, brackish, and non-Jamaican land mollusks described by C.B. Adams. Occasional Papers on Mollusks 3(43): 193–233 (including pls. 36–42).

Johnson, R.I. 1972c [5 June]. The Unionidae (Mollusca: Bivalvia) of peninsular Florida. Bulletin of the Florida State Museum, Biological Sciences 16(4): 181–249 [see 1972d (next entry) for the index].

Johnson, R.I. 1972d [July]. Errata [Index to unionid taxa in Johnson, "The Unionidae (Mollusca: Bivalvia) of peninsular Florida" (1972c)]. Priv. publ., 2 pp.

Johnson, R.I. 1972e [July]. Index to "Freshwater Mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwanee River," by William J. Clench and Ruth D. Turner [1956]. Priv. publ., 4 pp.

Johnson, R.I. 1973a [30 May]. The types of Unionidae (Mollusca: Bivalvia) described by C. S. Rafinesque in the Museum National d'Histoire Naturelle, Paris. Journal de Conchyliologie 110(2): 35–37, pl. 1.

Johnson, R.I. 1973b [29 June]. Distribution of Hydrobiidae, a family of fresh and brackish water gastropods, in peninsular Florida. Occasional Papers on Mollusks 3(46): 281–303 (including pls. 49–53).

Johnson, R.I. 1973c [29 June]. Clarke, Arthur H. 1973, *The freshwater molluscs of the Canadian interior basin* [book review]. Occasional Papers on Mollusks 3(46): 304.

Johnson, R.I. 1973d [December]. Heude's molluscan types, or, Asian land and fresh water mollusks, mostly from the People's Republic of China, described by P. M. Heude. Special Occasional Publication, Museum of Comparative Zoology, Department of Mollusks 1: 1–111 [MCZ Library received 3 December 1973; Library of Congress received 23 January 1974].

Johnson, R.I. and H.B. Baker, 1973e [27 December]. The types of Unionacea (Mollusca: Bivalvia) in the Academy of Natural Sciences of Philadelphia. Proceedings of the Academy of Natural Sciences of Philadelphia 125(9): 145–186 (including pls. 1–10).

Johnson, R.I. 1974a [April]. Examination of supposed types of fresh-water bivalves in Academy of Natural Sciences of Philadelphia. American Philosophical Society Year Book 1973: 316 [New Jersey Historical Society Library received 23 April 1974].

Johnson, R.I. 1974b [April]. Lea's unionid types or Recent and fossil taxa of Unionacea and Mutelacea introduced by Isaac Lea, including the location of all the extant types. Special Occasional Publication, Museum of Comparative Zoology, Department of Mollusks 2: 1–159 [reprinted 1992] [MCZ Library received 23 April 1974; Library of Congress received 13 May 1974].

Johnson, R.I. 1974c [April]. Marshall's unionid types or types of Recent and fossil Unionacea and Mutelacea introduced by William B. Marshall, including a bibliography of all his writings on mollusks. Special Occasional Publication, Museum of Comparative Zoology, Department of Mollusks 3: 1–14 [reprinted 1992] [MCZ Library received 23 April 1974; Library of Congress received 13 May 1974].

Johnson, R.I. 1974d [15 November]. Thomas Wyatt and Edgar Allan Poe, a pair of conchological plagiarists. Occasional Papers on Mollusks 4(50): 50–52.

Johnson, R.I. 1975a [1 October]. World's largest shell of the paper nautilus (*Argonauta argo* Linnaeus). Occasional Papers on Mollusks 4(51): 91–92.

Johnson, R.I. 1975b [1 October]. Unique purple shell of the paper nautilus (*Argonauta argo* Linnaeus). Occasional Papers on Mollusks 4(52): 103–104.

Johnson, R.I. 1975c [1 October]. R. Ellsworth Call with a bibliography of his works on mollusks and a catalogue of his taxa. Occasional Papers on Mollusks 4(54): 133–144 (including pl. 15).

Johnson, R.I. 1975d [1 October]. William A. Marsh, his introduced taxa of Unionidae or fresh water mussels. Occasional Papers on Mollusks 4(54): 145–147.

Johnson, R.I. 1975e [1 October]. *Cypraea leucodon* Broderip, rarest shell? Occasional Papers on Mollusks 4(54): 148.

Johnson, R.I. 1975f [October]. Simpson's unionid types and miscellaneous unionid types in the National Museum of Natural History. Special Occasional Publication, Museum of Comparative Zoology, Department of Mollusks 4: 1–57, pls. 1–3. [MCZ Library and Library of Congress both received 7 October 1975].

Johnson, R.I. 1975g [November]. First paper on the conchology of the United States by an American author, Thomas Say, 1817. Journal of the Society for the Bibliography of Natural History 7(3): 265–267 (including pl. 1).

Johnson, R.I. 1976a [February]. William Stimpson. Dictionary of Scientific Biography 13: 65–66 [library copy received 5 February 1976] [reprinted and condensed, 1981c].

Johnson, R.I. 1976b [April]. Richard Irwin Johnson. Pages 489–490, in (H. D. Lewis, ed.), Harvard Class of 1951 Twenty-Fifth Anniversary Report. Cambridge: Harvard Univ., xlviii + 1,114 pp.

Johnson, R.I. 1977a [21 October]. Monograph of the genus *Medionidus* (Bivalvia: Unionidae) mostly from the Apalachicolan region, southeastern United States. Occasional Papers on Mollusks 4(56): 161–187 (including pls. 17–19).

Johnson, R.I. 1977b [21 October]. Norman MacDowell Grier, a bibliography of his work on mollusks, with a catalogue of his unionid taxa. Occasional Papers on Mollusks 4(57): 226–227.

Johnson, R.I. 1977c [21 October]. Arnold Edward Ortmann, a bibliography of his work on mollusks, with a catalogue of his Recent molluscan taxa. Occasional Papers on Mollusks 4(58): 229–241 (including pls. 26–27).

Johnson, R.I. 1977d [21 October]. The Carnegie Museum, its collections and curators of mollusks. Occasional Papers on Mollusks 4(58): 242–244.

Johnson, R.I. 1978 [4 April]. Systematics and zoogeography of *Plagiola* (= *Dysnomia* = *Epioblasma*), an almost extinct genus of freshwater mussels (Bivalvia: Unionidae) from middle North America. Bulletin of the Museum of Comparative Zoology 148(6): 239–321 (including pls. 1–15).

Johnson, R.I. 1979 [21 December]. The types of Unionacea (Mollusca: Bivalvia) in the Museum of Zoology, the University of Michigan. Malacological Review 12(1–2): 29–36.

Johnson, R.I. 1980a [16 September]. Zoogeography of North American Unionacea (Mollusca: Bivalvia) north of the maximum Pleistocene glaciation. Bulletin of the Museum of Comparative Zoology 149(2): 77–189 (including pls. 1–20).

Johnson, R.I. 1980b [19 December]. The types of Unionacea (Mollusca: Bivalvia) in the Academy of Natural Sciences of Philadelphia: additions and corrections. Proceedings of the Academy of Natural Sciences of Philadelphia 132: 277–278.

Johnson, R.I. 1981a [27 March]. Stanley Truman Brooks, a bibliography of his work on mollusks with a catalogue of his molluscan taxa. Occasional Papers on Mollusks 4(59): 266–268.

Johnson, R.I. 1981b [27 March]. Recent and fossil Unionacea and Mutelacea (freshwater bivalves) of the Caribbean islands. Occasional Papers on Mollusks 4(60): 269–288 (including pls. 37–39).

Johnson, R.I. 1981c [14 October]. Stimpson, William. Page 657, in (J. F. Maurer et al., eds.), Concise Dictionary of Scientific Biography. New York: Charles Scribner's Sons, x + 773 pp. [condensed from 1976a, and without authorship attribution].

Johnson, R.I. and A. H. Clarke, Jr., 1983a [22 July]. A new spiny mussel, *Elliptio* (*Canthyria*) *steinstansana* (Bivalvia: Unionidae), from the Tar River, North Carolina. Occasional Papers on Mollusks 4(61): 289–298 (including pl. 40).

Johnson, R.I. 1983b [22 July]. *Margaritifera marrianae*, a new species of Unionacea (Bivalvia: Margaritiferidae) from the Mobile-Alabama-Coosa and Escambia River systems, Alabama. Occasional Papers on Mollusks 4(62): 299–304 (including pl. 41).

Johnson, R.I. 1984a [17 October]. A new mussel, *Lampsilis* (*Lampsilis*) *fullerkati* (Bivalvia: Unionidae) from Lake Waccamaw, Columbus County, North Carolina, with a list of the other unionid species of the Waccamaw River system.

Occasional Papers on Mollusks 4(63): 305–319 (including pls. 42–43).
Johnson, R.I. and K.J. Boss, 1984b [17 October]. *Fusconaia collina* (Conrad), from the James River, Virginia, an additional note. Occasional Papers on Mollusks 4(63): 319–320.
Johnson, R.I. 1984c [17 October]. Dates of publication of the molluscan portion (including the brachiopods) of the "*Fauna del Regno di Napoli*" (1829–1886) by Oronzio Gabriele Costa and Achille Costa. Occasional Papers on Mollusks 4(64): 330–332.
Johnson, R.I. 1984d [17 October]. Miscellany [Ignaz Edler von Born]. Occasional Papers on Mollusks 4(65): 348.
Johnson, R.I. 1984e [17 October]. The first popular shell book. Occasional Papers on Mollusks 4(66): 412.
Johnson, R.I. 1986 [April]. Richard Irwin Johnson. Pages 94–95, in (H. D. Lewis, ed.), Harvard Class of 1951 Thirty-Fifth Anniversary Report. Cambridge: Harvard Univ., [xxxvi] + 238 pp.
Johnson, R.I. 1989 [30 August]. Molluscan taxa of Addison Emery Verrill and Katharine Jeannette Bush, including those introduced by Sanderson Smith and Alpheus Hyatt Verrill. Occasional Papers on Mollusks 5(67): 1–143 (including pls. 1–19) [see 1997b and 1998b for updates].
Johnson, R.I. 1991a [April]. Richard Irwin Johnson. Pages 93–94, in (F. V. Fortmiller and H. D. Lewis, eds.), Harvard College Class of 1951 Fortieth Anniversary Report. Cambridge: Harvard Univ., [xlv] + 233 pp.
Roosevelt, A. C., R. A. Housley, M. I. da Silveira, S. Maranca, and R.I. Johnson, 1991b [13 December]. Eighth millennium pottery from a prehistoric shell midden in the Brazilian Amazon. Science 254(5038): 1621–1624.
Johnson, R.I. 1994a [June]. [Correction of] "A survey of the unionid fauna of the Susquehanna River Basin in Pennsylvania," by Arthur E. Bogan. Triannual Unionid Report (Freshwater Mollusk Conservation Society) 4: [5] [unpaginated].
Johnson, R.I. 1994b [7 December]. Types of shelled Indo-Pacific mollusks described by W. H. Pease. Bulletin of the Museum of Comparative Zoology 154(1): 1–61 (including pls. 1–10).
Johnson, R.I. 1996a [April]. Richard Irwin Johnson. Pages 83–84, in (H. D. Lewis and F. V. Fortmiller, eds.), Harvard College Class of 1951 Forty-Fifth Anniversary Report. Cambridge: Harvard Univ., xli + 236 pp.
Johnson, R.I. 1996b [20 November]. Types of land and freshwater mollusks from the Hawaiian Islands in the Museum of Comparative Zoology. Bulletin of the Museum of Comparative Zoology 155(4): 159–214.
Johnson, R.I. 1997a [1 August]. Comments on "The final report" of a massive search for *Lasmigona decorata* (Lea, 1852) and *Alasmidonta robusta* Clarke, 1981 (Bivalvia: Unionidae) from the Carolinas. Occasional Papers on Mollusks 5(71): 371–377 (including pl. 20).
Johnson, R.I. 1997b [1 August]. An overlooked northern European marine gastropod, *Omalaxis sarsi* Bush, 1897. Occasional Papers on Mollusks 5(71): 378 [update to 1989].
Johnson, R.I. 1997c [5 September]. Maine's Portland Society of Natural History. Northeastern Naturalist 4(3): 189–196.
Johnson, R.I. 1998a [30 January]. A new mussel, *Potamilis metnecktayi* (Bivalvia: Unionidae) from the Rio Grande system, Mexico and Texas with notes on Mexican *Disconaias*. Occasional Papers on Mollusks 5(76): 427–455 (including pls. 22–27).
Johnson, R.I. 1998b [30 January]. The myth of *Octopus giganteus* Verrill, 1897: a whale of a story. Occasional Papers on Mollusks 5(76): 456–457 [update to 1989].
Johnson, R.I. 1998c [30 January]. On "*The Chambered Nautilus*" by Oliver Wendell Holmes. Occasional Papers on Mollusks 5(76): 458–464 [see 1999g for update].
Johnson, R.I. 1998d [30 January]. On the provenance of certain books in the Department of Mollusks. Occasional Papers on Mollusks 5(76): 466–467 [see 1999f for update].
Johnson, R.I. 1998e. Addenda to be included with "Lea's figured unionid types" (1974). Museum of Comparative Zoology, Department of Mollusks, 2 pp. [supplement to 1974b].
Johnson, R.I. 1999a. Addenda to be included with: "Heude's Molluscan types" (1973). Museum of Comparative Zoology, Department of Mollusks, 1 pp. [supplement to 1973d].
Johnson, R.I. 1999b [30 August]. Unionidae of the Rio Grande (Rio Bravo del Norte) system of Texas and Mexico. Occasional Papers on Mollusks 6(77): 1–65 (including pls. 1–7).
Johnson, R.I. 1999c [30 August]. Taxa omitted from "Unionacea" by Fritz Haas, 1969. Occasional Papers on Mollusks 6(77): 66.
Johnson, R.I. 1999d [30 August]. The Duchess, the Brahmin, and the chank shell. Occasional Papers on Mollusks 6(78): 67–81.
Johnson, R.I. 1999e [30 August]. On the authorship of the first American conchological manual, John Warren's "*The Conchologist*." Occasional Papers on Mollusks 6(78): 81–88.
Johnson, R.I. 1999f [30 August]. On the provenance of certain books in the Department of Mollusks: alas, a correction and additional notes on John Clarkson Jay. Occasional Papers on Mollusks 6(78): 89–91 [update to 1998d].
Johnson, R.I. 1999g [30 August]. On "*The Chambered Nautilus*" by Oliver Wendell Holmes: redux. Occasional Papers on Mollusks 6(78): 92–95 [update to 1998c].
Johnson, R.I. 1999h [30 August]. *The Ambonese Curiosity Cabinet, by Georgius Everhardus Rumphius*, translated, edited, annotated, and with an introduction by E. M. Beekman [book review]. Occasional Papers on Mollusks 6(78): 96–105.
Johnson, R.I. 2001 [April]. Richard Irwin Johnson. Pages 256–258 and pl. 47, in (H. D. Lewis and F. V. Fortmiller, eds.), Harvard Class of 1951 Fiftieth Anniversary Report. Cambridge: Harvard Univ., lxxvii + 572 pp., 60 pls.
Johnson, R.I. 2002a [11 March]. Albert Gallatin Wetherby: malacology at the Cincinnati Society of Natural History and in Ohio (1843–1896). Occasional Papers on Mollusks 6(79): 109–133.
Johnson, R.I. 2002b [11 March]. Earliest American natural history lithograph. Occasional Papers on Mollusks 6(79): 133–134.
Johnson, R.I. 2002c [11 March]. Arthur Fairfield Gray (1855–1944), his malacological contributions. Occasional Papers on Mollusks 6(80): 135–147.
Johnson, R.I. 2002d [11 March]. The mollusk collection of the Boston Society of Natural History and its disposition. Occasional Papers on Mollusks 6(80): 148.
Johnson, R.I. 2002e [11 March]. The marvelous, monstrous, mythical, marine mollusk, *Cochlea sarmatica* Thevet, 1575. Occasional Papers on Mollusks 6(81): 149–163.
Johnson, R.I. 2002f [11 March]. The type material of *Cypraea semiplota* Mighels, 1845 (Gastropoda: Cypraeidae). Occasional Papers on Mollusks 6(81): 164–168 [supplement to 1949b].

Johnson, R.I. 2002g [11 March]. On the cunning character of a couple of conchologist collectors, Wesley Newcomb and William Harper Pease. Occasional Papers on Mollusks 6(81): 168–173.
Johnson, R.I. 2002h [11 March]. First colored illustrations of shells in the United States. Occasional Papers on Mollusks 6(81): 174.
Johnson, R.I. 2002i [11 March]. Samuel Liberty Harvey Fuller (1942–2001). Occasional Papers on Mollusks 6(82): 212.
Johnson, R.I. and W.J. Clench, 2002j [25 March]. Additions and corrections to Clench and Turner, 1962, New names introduced by H. A. Pilsbry. Museum of Comparative Zoology, Department of Mollusks, 22 pp.
Johnson, R.I. 2002k [31 December]. Samuel Liberty Harvey Fuller (1942–2001): a biographical sketch and his works on malacology. The Nautilus 116(4): 132–137.
Knudsen, J., K. R. Jensen, C. Nielsen and R.I. Johnson, 2003a [May]. Lorentz Spengler's descriptions of freshwater mussels (Mollusca: Unionacea): translation and notes. Steenstrupia 27(2): 263–279.
Johnson, R.I. 2003b [2 September]. Molluscan taxa and bibliographies of William James Clench and Ruth Dixon Turner. Bulletin of the Museum of Comparative Zoology 158(1): iv + 1–46.
Johnson, R.I. 2004 [31 March]. The rise and fall of the Boston Society of Natural History. Northeastern Naturalist 11(1): 81–108.
Johnson, R.I. 2006a [April]. Richard Irwin Johnson. Page 78, in (H. D. Lewis, ed.), Harvard College Class of 1951 Fifty-Fifth Anniversary Report. Cambridge: Harvard Univ., xvi + 206 pp.
Johnson, R.I. 2006b [19 December]. Conchology at the Lyceum of Natural History of New York, 1817–1876. Sporadic Papers on Mollusks 1: 3–53.
Johnson, R.I. 2006c [19 December]. John du Pont and other natural history museum related murders. Sporadic Papers on Mollusks 1: 54–63.
Johnson, R.I. 2006d [19 December]. Dates of the plates describing the mollusks collected on the *"Voyage au pôle sud et dans l'Océanie sur les corvettes l'Astrolabe et l'Zélée exécuté par ordre du Roi pendant les années 1837–1838–1839–1840 sous le commandement de M. Dumont d'Urville ..."* by Hombron and Jacquinot. Sporadic Papers on Mollusks 1: 64–66.
Johnson, R.I. 2006e [19 December]. Joseph Pitty Couthouy (1808–1864) and the United States Exploring Expedition: a second look. Sporadic Papers on Mollusks 1: 67–70.
Johnson, R.I. 2006f [19 December]. *Fusconaia* (*Lexingtonia*) *collina* (Conrad, 1836), no longer an endemic, but a probable example of stream capture. Sporadic Papers on Mollusks 1: 71.
Johnson, R.I. 2006g [19 December]. Joseph Charles Bequaert (1886–1982): his malacological contributions. Sporadic Papers on Mollusks 2: 73–107.
Johnson, R.I. 2006h [19 December]. William J. Clench and Ruth D. Turner, with a personal perspective on the Department of Mollusks, Museum of Comparative Zoology. Sporadic Papers on Mollusks 3: 111–166.
Johnson, R.I. 2006i [19 December]. David Humphreys Storer (1804–1891): the conchological phase. Sporadic Papers on Mollusks 3: 167–173.
Johnson, R.I. 2007 [10 December]. The conchologist as reluctant warrior. Pp. 219–222, in (D. Nenneman, ed.), The Harvard College Class of 1951: in the nation's service. Cambridge: priv. publ., xix + 449 pp.
Kabat, A.R. and R.I. Johnson, 2008 [9 June]. Dwight Willard Taylor (1932–2006): his life and malacological research. Malacologia 50(1–2): 175–218.
Johnson, R.I. 2009 [1 June]. Dwight Blaney and William Procter on the molluscan faunas of Frenchman Bay and Ironbound Island, Maine. Northeastern Naturalist 16, Monograph 4: 1–39.
Johnson, R.I. 2010a [January]. In memoriam, Arthur S. Merrill, 1916–2009. National Shellfisheries Association Quarterly Newsletter, January 2010: 4.
Johnson, R.I. 2010b [1 April]. In memoriam, Arthur Stewart Merrill, 1916–2009. Journal of Shellfish Research 29(1): 1–5.
Johnson, R.I. 2011 [April]. Richard I. Johnson. Pages 71–72, in (H. D. Lewis, ed.), Harvard College Class of 1951 Sixtieth Anniversary Report. Cambridge: Harvard Univ., xlviii + 189 + xiii + 50 pp.
Kabat, A.R. and R.I. Johnson, 2015 [3 June]. Kenneth Jay Boss (1935–2014). Breviora 544: 1–20.
Johnson, R.I. 2016 [April]. Richard I. Johnson. Page 41, in (H. D. Lewis, ed.), Harvard College Class of 1951 Sixty-Fifth Anniversary Report. Cambridge: Harvard Univ., xvi + 136 + xi + 37 pp.

ACKNOWLEDGMENTS

For assistance with certain publications, I thank Arthur Bogan (North Carolina Museum of Natural Sciences), Ronnie Broadfoot and Mary Sears (Ernst Mayr Library, MCZ), James Harney (Library, Harvard Club of New York), Nathan Smith (Library of Congress), and Scott Vile (Ascensius Press). For information on several aspects of Harvard and Radcliffe history and publications, I thank Joan Cotton (Radcliffe '51), Frederick Fortmiller (Harvard '51), and Deborah Smullyan (Harvard Alumni Association). Ieva Roznere checked the specimens of *Elliptio steinstansana* at the Ohio State University, and Jean-Marc Gagnon checked the type material of *Malletia johnsoni* at the National Museums of Canada. Eichhorst (2020) and Jenkinson (2020) have published short obituary notes, based in part on information provided by me. Several colleagues kindly shared their reminiscences, including George Buckley, Robert Chellis, Peter Dance, Thomas Hansen, James Mathewson, and Doug Smith. Arthur Bogan and an anonymous reviewer provided helpful comments that improved the manuscript. Dan Graf expertly prepared the plates.

LITERATURE CITED

Ambler, L.T., 1973. About those rhinos. Harvard Library Bulletin 21(3): 271–276, pls. 1–4.
Anonymous, 1942. The Blue Print [yearbook]. Belmont (Massachusetts): Belmont High School, 119 pp.
Anonymous, 1948. Harvard Yale Regatta, June 25, 1948 Official Program. New Haven (Connecticut): Yale Athletic Association, 48 pp.

Anonymous, 1954a. Engagements: Miss Marjory Weld Austin, Richard Irwin Johnson. New York Herald Tribune, 5 February 1954, p. 11.

Anonymous, 1954b. Marjory Austin to wed March 27; former embassy aide in Rome engaged to Richard Johnson, Harvard '51. New York Times, 14 February 1954, p. 90.

Anonymous, 1954c. Miss Austin betrothed. The Sun (Baltimore), 14 February 1954, p. S-12.

Anonymous, 1954d. Engagement announcements: Marjory Austin – Richard Johnson. Washington Post, 2 March 1954, p. 27.

Anonymous. 1954e. Post-debutante Marjory Austin weds Richard Johnson of Belmont. Boston Globe, 28 March 1954, p. A-4.

Anonymous. 1954f. Miss Marjorie [*sic*] Austin wed. The Sun (Baltimore), 28 March 1954, p. SC 12.

Anonymous. 1954g. Marjory W. Austin, bride of Richard Irwin Johnson. New York Herald Tribune, 7 April 1954, p. 21.

Anonymous. 1988. Marjory Johnson, 61, proprietor of antiques store. Boston Globe, 15 December 1988, p. 79.

Anonymous. 2014. Johnson, Marrian G. Boston Globe, 9 March 2014, p. B-8.

Anonymous. 2020a. Highlights from the conchology collection of the late Richard I. Johnson. Pp. 70–128, inside front cover and outside back cover, in: Americana, Travel and Natural History, New York, October 21, 2020 [auction catalog]. New York: Bonhams, 130 + [x] pp.

Anonymous. 2020b. Early printed books and illuminated manuscripts: property from the Estate of Richard I. Johnson. Pp. 2–15 and outside front cover, in: Fine Books and Manuscripts, New York, December 11, 2020 [auction catalog]. New York: Bonhams, 136 + [viii] pp. [in addition to the books identified as from the Johnson library (lots 1–7), lots 35, 43, 46, 80, 81, and 98 are also from his library].

Atlas, J. 2012. Between the lines of Harvard's Red Book. New York Times, 15 April 2012, Style section, pp. 1–2.

Baer, T.W. 1999. La rencontre de l'aventurier et de l'érudit. Bulletin de la Société Internationale de Conchyliologie 21(2): 2–10.

Benton, N. 2004. The seven Weld brothers … 1800 to 2000; a contemporary genealogy. New York: iUniverse, xxix + 211 pp.

Bogan, A.E. and W.R. Hoeh. 1995 ["1993–1994"]. *Utterbackia peninsularis*, a newly recognized freshwater mussel (Bivalvia: Unionidae: Anodontinae) from peninsular Florida, U.S.A. Walkerana þ7(17–18): 275–287.

Bosman, B. et al. 2015. Host confirmed for *Potamilus amphichaenus* and *Potamilus metnecktayi*. Ellipsaria (Freshwater Mollusk Conservation Society) 17(4): 15–16.

Boss, K.J. 1998. Richard Irwin Johnson. Occasional Papers on Mollusks 5: ii–ix.

Brown, D.J. 2013. The boys in the boat: nine Americans and their epic quest for gold at the 1936 Berlin Olympics. New York: Viking, [viii] + 404 pp.

Buckley, G. 2020. Richard I. Johnson (1925–2020). The Epitonium, Newsletter of the Boston Malacological Club, Summer 2020: 6.

Bunting, B. (ed. M. H. Floyd), 1985. Harvard: an architectural history. Cambridge: Harvard Univ. Press, xiv + 350 pp.

Cain, V. 2017. Present tense: locating history in Boston's museums of science. Isis 108(2): 381–389.

Carlson, M.F. 1955. Boston Malacological Club. American Malacological Union, Annual Report 1954: 29.

Clarke, A.H. Jr. 1961. Abyssal mollusks from the south Atlantic Ocean. Bulletin of the Museum of Comparative Zoology 125(12): 345–387.

Clench, W.J. 1940. Report on Mollusks. Pages 30–33, in (T. Barbour, ed.), Annual Report of the Director of the Museum of Comparative Zoölogy at Harvard College to the President of Harvard College for 1939–1940, 66 pp.

Clench, W.J. 1943. [Report on Mollusks]. Pp. 14–15, in (T. Barbour, ed.), Annual Report of the Director of the Museum of Comparative Zoölogy at Harvard College to the President of Harvard College for 1942–1943, 28 pp.

Coan, E.V. and M.G. Harasewych. 1993. Publication dates of *The Nautilus*. The Nautilus 106(4): 174–180.

Coan, E.V. and A.R. Kabat. 2007. The publications of the American Malacological Union / Society. American Malacological Bulletin 23: 1–10.

Coan, E.V. and A.R. Kabat. 2012. The malacological works and taxa of Sylvanus Hanley (1819–1899). Malacologia 55(2): 285–359.

Crowley, B.S. 1963. Boston Malacological Club. American Malacological Union, Annual Reports for 1963: 52.

Culligan, D. 1957. Boston Malacological Club. American Malacological Union, Annual Report 1956: 36.

Dance, S.P. 1986. A history of shell collecting. Leiden: E. J. Brill – W. Backhuys, xv + 265 pp., 32 pls.

Dance, S.P. 2009. A name is a name is a name: some thoughts and personal opinions about molluscan scientific names. Zoologische Mededelingen 83(7): 565–576 [translated into Chinese, Shell Discoveries 1(1): 4–8 (2012)].

Danzig, A. 1948. Harvard varsity crew nips Yale in stirring 4-mile race. New York Times, 26 June 1948, p. 13.

Dean, R. 1999. Mirthful conchologists. Harvard Magazine 101(4): 12, 97 [letter to the editor].

Drury, S.S. 1964. Crew. Pp. 565–637, in (G. H. Movius, ed.), The second H book of Harvard Athletics 1923–1963. Cambridge: Harvard Varsity Club, xvii + 941 pp.

Eichhorst, T. (ed.) 2020. Richard Irwin Johnson (1925–2020). American Conchologist 48(3): 22–23 [based on Boss, 1998 and A. R. Kabat, in litt.].

Farrell, M.F. 1952. Boston Malacological Club. American Malacological Union, News Bulletin and Annual Report 1951: 26.

Farrell, M.F. 1954. Boston Malacological Club. American Malacological Union, Annual Report 1953: 38.

Finet, Y. and H. Watzlawick. 1999. Un docte ennuyeux retrouvé. L'Intermédiaire des Casanovistes (Genève) 16: 33–34.

Graf, D.L. 2013. Patterns of freshwater bivalve global diversity and the state of phylogenetic studies on the Unionoida, Sphaeriidae, and Cyrenidae. American Malacological Bulletin 31(1): 135–153.

Graf, D.L. and K.S. Cummings. 2009. Actual and alleged freshwater mussels (Mollusca: Bivalvia: Unionoida) from Madagascar and the Mascarenes, with description of a new genus, *Germainaia*. Proceedings of the Academy of Natural Sciences of Philadelphia 158: 221–238.

Harris, C.M. 1977. Williams, Ben Ames. Pp. 747–748, in (J. A. Garraty, ed.), Dictionary of American Biography, Supplement Five, 1951–1955. New York: Charles Scribner's Sons, x + 799 pp.

Hunter, T.H. 1948. Harvard rowing 1923–1940. Pp. 119–132, in (R. F. Herrick, ed.), Red Top: Reminiscences of Harvard rowing. Cambridge: Harvard Univ. Press, vi + 255 pp.

ICZN. 1999. International Code of Zoological Nomenclature (4th ed.). London: International Trust for Zoological Nomenclature, xxix + 306 pp.

ICZN. 2003. Declaration 44: Amendment of Article 74.7.3. Bulletin of Zoological Nomenclature 60(4): 263.

Jenkinson, J.J. ed., 2020. Obituary: Richard Irwin Johnson, 1925–2020. Ellipsaria (Freshwater Mollusk Conservation Society) 22(3): 21–22 [based on Boss, 1998 and A. R. Kabat, in litt.].

Karatayev, A.Y., T.D. Miller, and L.E. Burlakova. 2012. Long-term changes in unionid assemblages in the Rio Grande, one of the world's top 10 rivers at risk. Aquatic Conservation: Marine and Freshwater Ecosystems 22(2): 206–219.

La Perna, R. 2003. The Quaternary deep-sea protobranch fauna from the Mediterranean: composition, depth-related distribution and changes. Bollettino Malacologico 39(1–4): 17–34.

Lighthill, D.P. ed., 1951. Harvard 1951 [yearbook]. Cambridge: Harvard Yearbook Publications, 316 pp.

Little, D.B. (ed.) 1987. The centennial book. Boston: Club of Odd Volumes, 143 pp.

Lopes-Lima, M. et al. 2018. Expansion and systematics redefinition of the most threatened freshwater mussel family, the Margaritiferidae. Molecular Phylogenetics and Evolution 127: 98–118.

Marius, R.C. 1994. Minutes, The Club of Odd Volumes, April 20, 1994. Boston: Club of Odd Volumes (priv. printed), 6 pp.

Marquard, B. 2011. Dr. Allen Crocker, 85; offered care and hope to children with Down syndrome. Boston Globe, 18 November 2011, p. B-14.

Mathewson, J. 2020. [Class Notes for 1951]. Harvard Magazine 123(1): 60-A.

Maynard, D.M. ed., 1948. The 1951 Harvard Freshman Red Book (vol. 39). Cambridge: Harvard Univ., 171 pp.

McCallum, G. 1960. Boston Malacological Club. American Malacological Union, Annual Report 1959: 58.

McCartney, M.A. et al. 2016. Phylogenetic analysis of Lake Waccamaw endemic freshwater mussel species. American Malacological Bulletin 34(2): 109–120.

McMichael, D.F. 1956. Notes on the freshwater mussels of New Guinea. The Nautilus 70(2): 38–48, pl. 2.

McMichael, D.F. and I.D. Hiscock, 1958. A monograph of the freshwater mussels (Mollusca: Pelecypoda) of the Australian region. Australian Journal of Marine and Freshwater Research 9(3): 372–508, pls. 1–19.

Mitchell, J.H. 2005. Looking for Mr. Gilbert: the reimagined life of an African American. Washington, D.C.: Shoemaker Hoard, [iv] + 278 + [ii] pp.

Pennington, B. 2020. The quest for football's Holy Grail. New York Times, 2 February 2020, Sports section, pp. 8–9.

Perkins, M.A., N.A. Johnson, and M.M. Gangloff, 2017. Molecular systematics of the critically-endangered North American spinymussels (Unionidae: *Elliptio* and *Pleurobema*) and description of *Parvaspina* gen. nov. Conservation Genetics 18(4): 745–757.

Pfeiffer, J.M., J. W. Breinholt, and L.M. Page. 2019. Unioverse: a phylogenetic resource for reconstructing the evolution of freshwater mussels (Bivalvia, Unionoida). Molecular Phylogenetics and Evolution 137: 114–126.

Pick, N. 2004. The rarest of the rare: stories behind the treasures at the Harvard Museum of Natural History. New York: Harper Collins, xiv + 178 pp.

Pierce, S.K. et al. 1995. On the giant octopus (*Octopus giganteus*) and the Bermuda Blob: homage to A.E. Verrill. Biological Bulletin 188(2): 219–230.

Pierce, S.K. et al. 2004. Microscopic, biochemical, and molecular characteristics of the Chilean Blob and a comparison with the remains of other sea monsters: nothing but whales. Biological Bulletin 206(3): 125–133.

Provine, W.B. 1986. In praise of scientific reprint collections. Pp. 2–4, in (E. C. Carter II, ed.), Scientific reprint collections: a conference sponsored by the American Philosophical Society Library April 1984. Philadelphia: American Philosophical Society Library, ii + 19 pp.

Reed, C. 1998. A visit to the Mollusk Department: Richard I. Johnson '51 has passed 60 years in unamphibological celebration of the freshwater bivalves. Harvard Magazine 101(2): 106–109. https://www.harvardmagazine.com/sites/default/files/html/1998/nd98/alumni.mollusk.html

Rheault, C. ed. 2004. A chronicle 1987–2003. Boston: Club of Odd Volumes, 64 pp.

Sanders, H.L. and J.A. Allen. 1985. Studies on deep-sea Protobranchia (Bivalvia); the family Malletiidae. Bulletin of the British Museum (Natural History), Zoology 49(2): 195–238.

Scinto, L. F. M., ed., 2015. All members exhibition: my favorite things, December 2013 – March 2014. Boston: Club of Odd Volumes, 38 pp.

Sherman, M.W. 1954a. Society. Boston Globe, 5 February 1954, p. 25.

Sherman, M.W. 1954b. Society. Boston Globe, 26 March 1954, p. 20.

Smith, C.H. et al. 2019. Integrative taxonomy reveals a new species of freshwater mussel, *Potamilus streckersoni* sp. nov. (Bivalvia: Unionidae): implications for conservation and management. Systematics and Biodiversity 17(4): 331–348.

Smith, C.H., J.M. Pfeiffer, and N.A. Johnson, 2020. Comparative phylogenomics reveal complex evolution of life history strategies in a clade of bivalves with parasitic larvae (Bivalvia: Unionoida: Ambleminae). Cladistics 36(5): 505–520.

Smith, D.G. 2001. Systematics and distribution of the Recent Margaritiferidae. Pp. 33–49, in (G. Bauer and K. Wächtler, eds.), Ecology and evolution of the freshwater mussels Unionoida. Ecological Studies 145: xxii + 394 pp.

Souza, L.S. de and A.D. Pimenta. 2019. Taxonomy of littoral *Melanella* (Gastropoda: Eulimidae) from Brazil, with comments on the *Eulima* described by Verrill and Bush (1900). Marine Biodiversity 49: 425–442.

Walker, K.F. 2016. An interesting genus of freshwater mussels from Indonesian Papua, not seen by biologists for many years. Unitas Malacologica Newsletter 36: 18–21.

Wepman, D. 1999. Williams, Ben Ames. American National Biography 23: 431–432.

Williams, F.T. 1962. All about Da. Chestnut Hill (Mass.), priv. publ., [iv] + 293 pp.

Williams, J.D., A.E. Bogan, and J.T. Garner. 2008. Freshwater mussels of Alabama and the Mobile Basin in Georgia, Mississippi and Tennessee. Tuscaloosa: Univ. of Alabama Press, xv + 908 pp.

Williams, J.D., R.S. Butler, and J. M. Wisniewski. 2011. Annotated synonymy of the recent freshwater mussel taxa of the families Margaritiferidae and Unionidae described from Florida and drainages contiguous with Alabama and Georgia. Bulletin of the Florida Museum of Natural History 51(1): 1–84.

Williams, J.D. et al. 2017. A revised list of the freshwater mussels (Mollusca: Bivalvia: Unionoida) of the United States and Canada. Freshwater Mollusk Biology and Conservation 20(2): 33–58.

Yeung, N.W. et al. 2017. Type specimens of Hawaiian land snails in the Smithsonian Institution, National Museum of Natural History, with lectotype designations. Smithsonian Contributions to Zoology 647: 1–34.

RESEARCH NOTE

An unprecedented observation of the nudibranch *Spurilla braziliana* (Gastropoda: Aeolidiidae) as a food resource of the pycnogonid *Pigrogromitus timsanus* (Arthropoda: Ascorhynchoidea)

Licia Sales
Departamento de Zoologia, Instituto de Biociências
Universidade de São Paulo, São Paulo, BRAZIL

Vinicius Queiroz
Departamento de Fisiologia, Instituto de Biociências
Universidade de São Paulo, São Paulo, BRAZIL

Rudá A. Lucena
Programa de Pós-Graduação em Ciências Biológicas-Zoologia
Departamento de Sistemática e Ecologia
Universidade Federal da Paraíba, João Pessoa, BRAZIL

Alvaro E. Migoto
Centro de Biologia Marinha
Universidade de São Paulo, São Sebastião, BRAZIL

Since adult nudibranchs lack a shell they may appear vulnerable to predators. However, the wide array of defense mechanisms they employ, including crypsis, aposematic coloration, mimicry, and chemical defenses, among others (Behrens et al., 2005), are efficient anti-predatory strategies (see Rudman, 2000). In fact, few organisms can overcome such defenses and prey on nudibranchs (Valdés et al., 2013). These include other gastropods (Valdés et al., 2013), crustaceans (Anker and Ivanov, 2020), and pycnogonids (Piel, 1991).

Most reported cases of nudibranch predation by pycnogonids are from species of *Anoplodactylus* Wilson, 1878 (e.g., Piel, 1991; Rogers et al., 2000); there are also some reports of pycnogonids as parasites (e.g. Ohshima, 1933; Merton, 1906). However, most reports of pycnogonids as either predators or parasites are brief and generally poorly illustrated (e.g., Ohshima, 1933; Piel, 1991; Rogers et al., 2000).

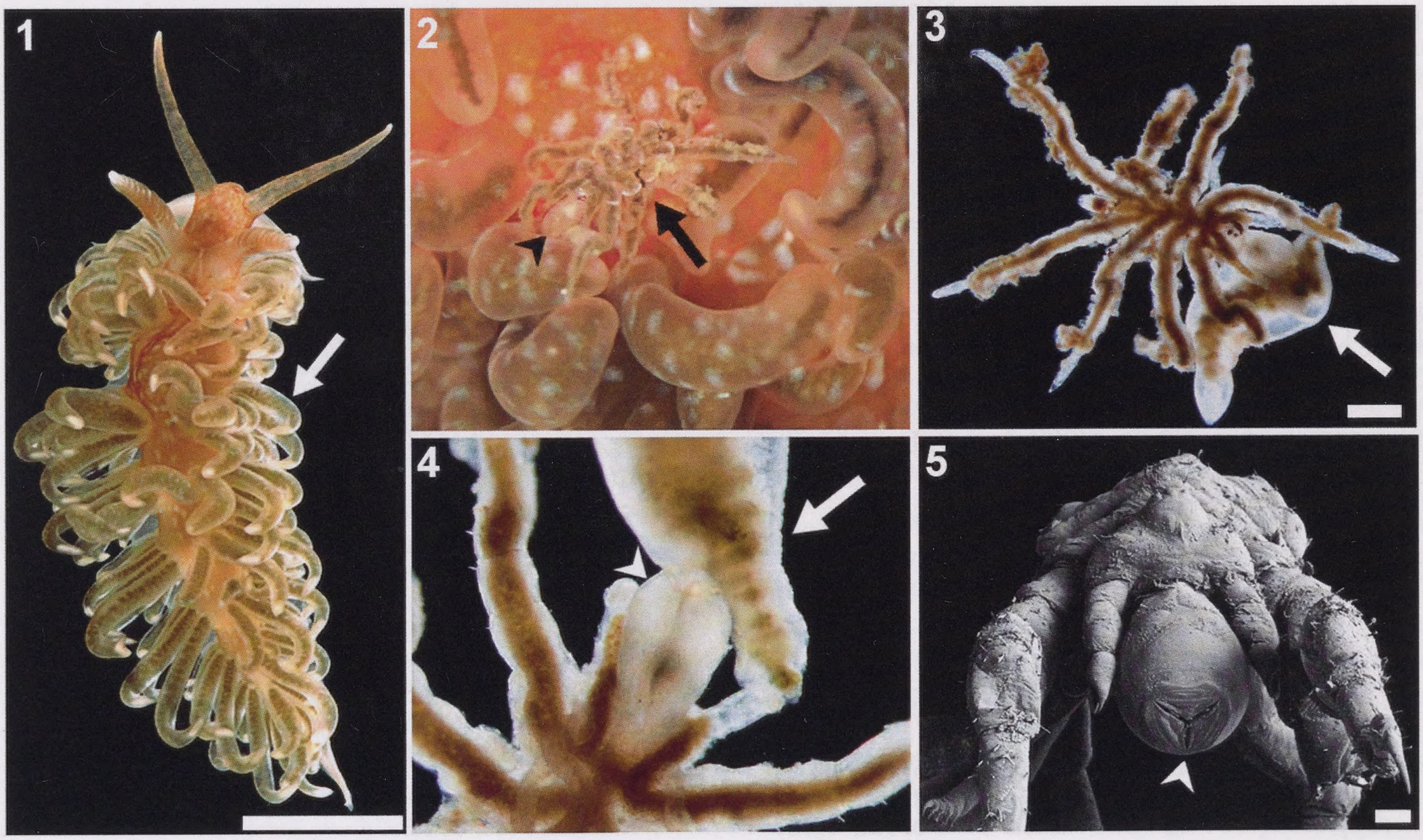
We report and illustrate for the first time the nudibranch *Spurilla braziliana* MacFarland, 1909 as a food source of the pycnogonid *Pigrogromitus timsanus* Calman, 1927, which is also the first record of this species feeding on a mollusk. Moreover, we discuss how pycnogonids seem to cope with nudibranch defenses.

In July 2017, eight specimens of *S. braziliana* (Figure 1) were collected at Araçá Bay (23° 48'47" S; 45°24'30" W), São Sebastião, Brazil, one of which (about 4 cm long) had a pycnogonid on its back (Figure 2). It was isolated in a plastic container (400 ml), at room temperature (24°C ±1°C), with the seawater changed daily. The nudibranch and pycnogonid were observed daily for the following ten days. The nudibranch was fed one sea anemone (*Bunodosoma caissarum* Corrêa in Belém, 1987 or *Anemonia sargassensis* Hargitt, 1908) every two days. The animals were imaged under a stereomicroscope Zeiss SV-11 coupled with a Sony NEX FS700 camera. The pycnogonid specimen was later fixed in 70% ethanol, dehydrated in a graded ethanol series until 100% ethanol, critical point dried using CO2 as intermediate, mounted on a stub, coated with gold, and photographed under a Zeiss Sigma VP scanning electron microscope (Zeiss, Germany).

Pigrogromitus timsanus (Figures 2–5) remained clinging to the back of *S. braziliana* during the whole period of observation (video record available at https://youtu.be/gpx6l9Au1zk), frequently seen sucking the nudibranch's cerata by attaching its proboscis to the base of a ceras (Figures 2–4). In an attempt to isolate *P. timsanus*, one ceras was removed along with the pycnogonid (Figures 3, 4), which continued to feed on the ceras' base (Figures 3, 4) for at least 16 min, when we stopped filming. As soon as *P. timsanus* was returned to the pot, it climbed to the back of *S. braziliana*. Although the nudibranch appeared healthy, it died for unknown reasons after 10 days. In contrast, the other specimens (n=7) of *S. braziliana* were in good condition—eating and behaving normally—for five more days, after which they were anesthetized with a mixture of isotonic magnesium chloride solution and menthol dissolved in seawater, and fixed in 70% ethanol.

The pycnogonid was always hanging on the dorsal area of *S. braziliana*, even when not feeding; when undisturbed, it did not cause autotomy or any remarkable damage to the nudibranch. Previous records showed that pycnogonids: (1) trigger cerata autotomy, then proceed to eat them, as observed in *Anoplodactylus californicus* Hall, 1912 (= *A. carvalhoi* Marcus, 1940) preying on *Dondice occidentalis* (Engel, 1925) (Piel, 1991); (2) insert their proboscis on the distal part of the nudibranch's papillae and release the prey at the end, as recorded to *A. longiceps* Stock, 1951 feeding on *Okenia* sp. (Arango and Brodie, 2003); or (3) consume entire small (< 10mm) individuals, as reported to *A. evansi* Clark, 1963 preying on some sea slugs (Rogers et al., 2000).

The continuous clinging to and feeding on the nudibranch could initially be interpreted as parasitism, but such behavior could be induced by the lack of other place or animal to which the pycnogonid could attach or prey upon. Although there is one report of *P. timsanus* as a possible parasite of anemones (Mercier and Hamel, 1994), the species is generally reported as free-living, having already been found on a wide variety of habitats, including different invertebrates (e.g. Müller and Krapp, 2009). Even so, this is the first report of *P. timsanus*



Figures 1–5. Interactions between the nudibranch *Spurilla braziliana* and the pycnogonid *Pigrogromitus timsanus*. **1.** *Spurilla braziliana,* 4 cm long. **2.** *Pigrogromitus timsanus* crawling on *S. braziliana.* **3.** *Pigrogromitus timsanus* feeding on a detached ceras of *S. braziliana*. **4.** Detail of the pycnogonid's mouth attached to the ceras basis. **5.** Scanning electron microscope of *P. timsanus* showing its mouth aperture. Legend: white arrow = ceras; black arrow = *P. timsanus;* arrowhead = proboscis. Scale bars: (1) 1 cm; (3) 500 μm; (5) 100 μm.

found on a mollusk, indicating that this may not be common. Since *P. timsanus* has been reported feeding on sea anemones (Mercier and Hamel, 1994), and sea anemones are the food of *S. braziliana*, the pycnogonid may have accidentally moved from an anemone to the nudibranch during feeding; or considering the set of different habitats on which the pycnogonid has already been found, if it was a generalist feeder it could opportunistically move to and prey on the nudibranch. Assuming that a parasite is an organism that feeds intimately on one host during a life stage (Lafferty and Kuris, 2002), and that *S. braziliana* is not the first species reported as a food source for adult *P. timsanus*, we assume that the finding reported here is a case of micropredation, not parasitism. In such cases, the micropredator feeds on more than one prey during a life stage without necessarily eliminating the prey's fitness (Lafferty and Kuris, 2002).

There are two main behavioral strategies that pycnogonids seem to use to cope with nudibranch defenses: (1) avoid direct contact with defensive structures/substances (Arango and Brodie, 2003); (2) avoid eating more toxic individuals (Rogers et al., 2000). The first seems to be the case of *Anoplodactylus* spp. preying on dorid and aeolid nudibranchs. Dorid nudibranchs are known to have chemical defenses on the mantle (Cimino et al., 1999), while aeolids (as *S. braziliana*) acquire the nematocysts (microscopic stinging structures) from their cnidarian prey and store them at the tip of their cerata (Goodheart and Bely, 2016). Therefore, to feed on the tip of the dorid's papillae (Arango and Brodie, 2003) or to feed on the base of the aeolids' cerata (present study; Piel, 1991) may be a strategy to avoid the putative chemical defenses in the mantle structures (Arango and Brodie, 2003) or the nematocysts, respectively. However, the pycnogonid *A. evansi* can survive even after consuming entire nudibranchs, which matches the second strategy mentioned above. Rogers et al. (2000) proposed that by eating only small individuals, which may lack substantial amounts of diet-derived defenses, the pycnogonid could reduce possible damages. Moreover, it is possible that *A. evansi* may also use physiological strategies (i.e., isolating prey tissues with harmful substances in vacuoles during digestion) to deal with the toxic substances of its prey (Rogers et al., 2000).

For most pycnogonids, feeding habits and prey remain poorly known, with some cases of pycnogonid-host association interpreted as feeding relationships, even without direct feeding observations (Dietz et al., 2018). Similarly, little is known about nudibranch predators. Therefore, this

study adds to the knowledge of pycnogonids' feeding habits and preys, and of nudibranchs' predators, also providing the first filmed record of their interactions.

ACKNOWLEDGMENTS

The authors thank the technical staff of the Institute of Biosciences (IB) of the University of São Paulo (USP) for scanning electron microscopy. Licia Sales thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the grant that supported this study (CAPES – Finance Code 001). Vinicius Queiroz thanks FAPESP (Grant numbers: 2015/21460-5 and 2018/14497-8) for personal financial support. Rudá A. Lucena acknowledges a Doctoral scholarship from CAPES.

LITERATURE CITED

Anker, A. and Y. Ivanov. 2020. First record of the predation upon sea slugs (Cephalaspidea and Nudibranchia) by the peculiar elbow crab *Lambrachaeus ramifer* Alcock, 1895 (Decapoda: Parthenopidae). Marine Biodiversity 50: 24. doi.org/10.1007/s12526-020-01047-x

Arango, C.P. and G.D. Brodie. 2003. Observation of predation on the tropical nudibranch *Okenia* sp. by the sea spider *Anoplodactylus longiceps* Williams (Arthropoda: Pycnogonida). The Veliger 46: 99–101.

Behrens, D.W. 2005. Nudibranch Behavior. New World Publications, Inc., Florida, 176 pp.

Cimino, G., A. Fontana, and M. Gavagnin. 1999. Marine opisthobranch molluscs: chemistry and ecology in sacoglossans and dorids. Current Organic Chemistry 3(4): 327–372.

Dietz, L., J.S. Dömel, F. Leese, T. Lehmann, and R.R. Melzer. 2018. Feeding ecology in sea spiders (Arthropoda: Pycnogonida): what do we know? Frontiers in Zoology 15: 7 doi.org/10.1186/s12983-018-0250-4

Goodheart, J.A., and A.E. Bely. 2016. Sequestration of nematocysts by divergent cnidarian predators: mechanism, function, and evolution. Invertebrate Biology 136: 75–91.

Lafferty, K.D. and A.M. Kuris. 2002. Trophic strategies, animal diversity, and body size. Trends in Ecology & Evolution 17(11): 507–13.

Mercier, A. and J.F. Hamel. 1994. Deleterious effects of a pycnogonid on the sea anemone *Bartholomea annulata*. Canadian Journal of Zoology 72: 1362–13624.

Merton, H. 1906. Eine auf Tethys leporina parasitisch lebende Pantopodenlarve (*Nymphon parasiticum* n. sp.). Mittheilungen nus der Zoologischen Station Neapel 18: 136–41.

Müller, H.G. 1993. World catalogue and bibliography of the recent Pycnogonida. Germany: Wissenschaftlicher Verlag, 410 pp.

Müller, H.G. and F. Krapp. 2009. The pycnogonid fauna (Pycnogonida, Arthropoda) of the Tayrona National Park and adjoining areas on the Caribbean coast of Colombia. Zootaxa 2319: 1–138.

Ohshima, H. 1933. Young Pycnogonids found parasitic on nudibranchs. Annotationes Zoologicae Japonenses 14: 61–66.

Piel, W.H. 1991. Pycnogonid Predation on nudibranchs and ceratal autotomy. The Veliger 34: 366–367.

Rogers, C.N., R. de Nys. and P.D. Steinberg. 2000. Predation On juvenile *Aplysia parvula* and other small anaspidean, ascoglossan, and nudibranch gastropods by Pycnogonida. The Veliger 43: 330–337.

Rohde, K. 2005. Definitions and adaptations to a parasitic way of life. PP. 1–10 *in* Rohde, K (ed), Marine parasitology. Collingwood: CSIRO Publishing, 592 pp.

Rudman, W.B. 2000. What eats sea slugs? *In*: Sea Slug Forum. Australian Museum, Sydney (www.seaslugforum.net/find/predrecord) [accessed 17 December 2020]

Valdés, A., L. Blanchard, and W. Marti. 2013. Caught naked: First report a nudibranch sea slug attacked by a cone snail. American Malacological Bulletin 31(2): 337–338.

Sponsored in part by the State of Florida, Department of State, Division of Cultural Affairs and the Florida Council on Arts and Culture

CULTURE BUILDS FLORIDA

FLORIDA DEPARTMENT of STATE
DIVISION of CULTURAL AFFAIRS

INSTRUCTIONS TO AUTHORS

The Nautilus publishes articles on all aspects of the biology, paleontology, and systematics of mollusks. Manuscripts describing original, unpublished research and review articles will be considered. Brief articles, not exceeding 1000 words, will be published as Research Notes and do not require an abstract.

Manuscripts: Each original manuscript and accompanying illustrations should be submitted to the editor via e-mail. Authors should follow the general recommendations of Scientific Style and Format—The CSE Manual for Authors, Editors, and Publishers, available from the Council of Science Editors at http://www.scientificstyleandformat.org/Home.html.

The first mention of a scientific name in the text should be accompanied by the taxonomic authority, including year. Metric, not English, units are to be used. The sequence of sections should be Title, Author(s) and Affiliations, Abstract, Additional Keywords, Introduction, Materials and Methods, Results, Discussion, Conclusions, Acknowledgments, Literature Cited, Tables, Figure Captions, Figures. If the author for correspondence is not the senior author, please indicate in a footnote. The abstract should summarize in 250 words or less the scope, main results, and conclusions of the article. Abstracts should be followed by a list of additional keywords. All references cited in the text must appear in the Literature Cited section and vice-versa. Please follow a recent issue of *The Nautilus* for bibliographic style, noting that journal titles must be unabbreviated. Information on plates and figures should be cited only if not included within the pagination of cited work. Tables must be numbered and each placed on a separate page. If in doubt, please follow a recent issue of the journal for sequence of sections and other style requirements.

Illustrations: Illustrations are rendered either at full-page width (maximum width 17 cm) or column width (maximum width 8.2 cm). Please take these dimensions into consideration when preparing illustrations. Page-width illustrations ideally should span the entire width of printed page (17 cm). "Tall" page-width illustrations should be avoided, square or "landscape" formats work better. Please design plates accordingly, such that there will be enough space left at the bottom of printed page for plate caption. (Digital technology has made this task much easier.)

All line drawings must be in black, clearly detailed, and completely labeled. Abbreviation definitions must be included in the caption. Line drawings must be high resolution fi les at least 600 dpi (dots per inch) resolution at actual size. Standard digital formats for line drawings include .tif, .bmp, .psd, .eps, and .pdf.

Photographs may be submitted in black-and-white or color, preferably in RGB mode if in color. Standard digital formats for photographs include .tif, .psd, .jpg, or .pdf. Photographs must be high resolution files at least 300 dpi resolution at actual (printed) size.

If more than one figure is included in an illustration, all figures are to be consecutively numbered (Figures 1, 2, 3, . . . , NOT Figures 1A, 1B, 1C, . . . , NOR Plate 1, Figure 1, . . .). In illustrations with more than one figure, make sure that blank areas between figures should be kept to a minimum, thereby allowing for more area for each individual figure.

Compressed (e.g., .jpg) or other low-resolution file formats may be used to facilitate original submission and the review process, but may not be acceptable at final submission (see below).

Types and Voucher Specimens: Deposition of the holotype in a recognized institutional, public collection is a requirement for publication of articles in which new species-level taxa are described. Deposition of paratypes in institutional collections is strongly recommended, as is the deposition of representative voucher specimens for all other types of research work.

The Editorial Process: Upon receipt, all manuscripts are assigned a number and acknowledged. The editor reserves the right to return manuscripts that are substandard or not appropriate in scope for journal. Manuscripts deemed appropriate for the journal will be sent for critical review to at least two reviewers. The reviewers' recommendations will serve as basis for rejection or continuation of the editorial process. Reviewed manuscripts will be sent back to authors for consideration of the reviewers comments. The revised version of the manuscript may at this point be considered accepted for publication by the journal.

Final Submission: Authors of accepted manuscripts are required to submit a final version to the editor at jleal@shellmuseum.org. High-resolution image files may be sent to the editor at this stage.

Proofs: After typesetting, proofs will be sent to the author. Author should read proofs carefully and send corrections to the editor within 48 hours. Changes other than typesetting errors will be charged to the author at cost.

Offprints: An order form for offprints will accompany the proofs. Offprints will be ordered directly from the editor. Authors with institutional, grant, or other research support will be asked to pay for page charges at the rate of $60 per page.

More information at http://shellmuseum.org/learn/the-nautilus.

♾ This paper meets the requirements of ANSI/NISO Z39.48-1992 (Permanence of Paper)

SMITHSONIAN LIBRARIES
3 9088 02065 7516